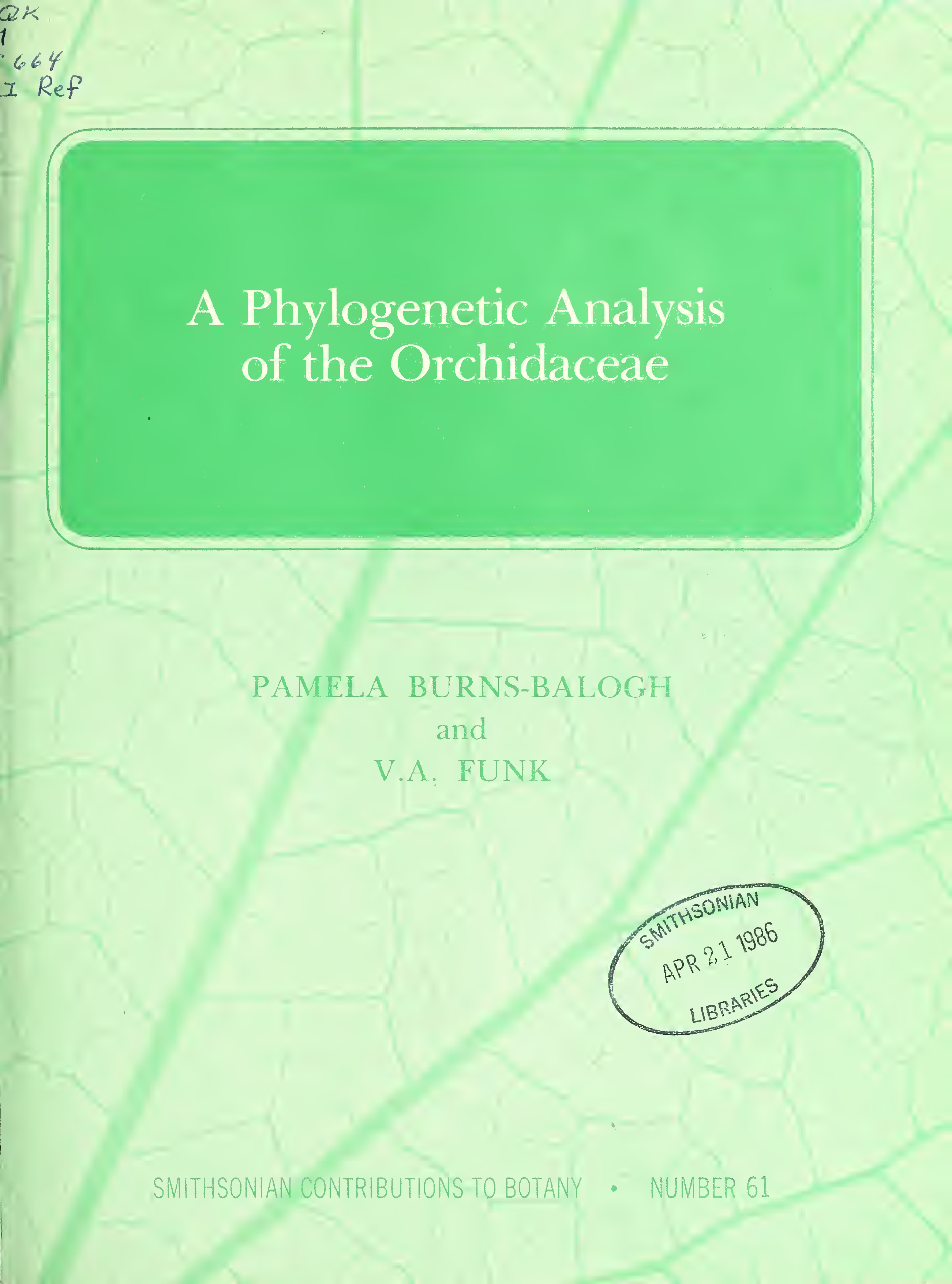

A Phylogenetic Analysis of the Orchidaceae

PAMELA BURNS-BALOGH
and
V.A. FUNK

SMITHSONIAN CONTRIBUTIONS TO BOTANY • NUMBER 61

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ABSTRACT

Burns-Balogh, Pamela, and V.A. Funk. A Phylogenetic Analysis of the Orchidaceae. *Smithsonian Contributions to Botany*, number 61, 79 pages, 94 figures, 4 plates, 1986.—The Orchidaceae is the largest flowering plant family, with approximately 25,000 species. Sixty-eight apomorphies grouped into forty-two transformation series were used to construct a cladogram for the twenty-six tribes of the family. A detailed discussion of the characters is followed by an in-depth analysis of the cladogram. The cladogram was used to develop a classification and a natural key to the tribes. Seven subfamilies (Neuwiedioideae, Apostasioideae, Cypripedioideae, Spiranthoideae, Neottioideae, Orchidoideae, and Epidendroideae) are divided into 20 tribes, the majority of which are defined by synapomorphies. Of the intrasubfamily classifications, that of the Epidendroideae is the most tenuous. The phylogeny and classification presented here are hypotheses of relationship and are therefore subject to change as more information becomes available.

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A Phylogenetic Analysis of the Orchidaceae

Pamela Burns-Balogh and V.A. Funk

Introduction

Traditionally, the orchids have been separated into two major groups (formal or informal) based on the number of anthers: monandrous and nonmonandrous (Pfitzer, 1888–1889; Schlechter, 1926). The monandrous orchids (one functional stamen) comprise the largest group, with approximately 25,000 species, and consist of the subfamilies Spiranthoideae, Orchidoideae, Epidendroideae and Vandoideae (for this section of the paper all categories are those of Dressler 1981; see Table 1). The second group contains orchids that have more than one functional stamen. This group is much smaller, with about 200 species in two subfamilies, the Apostasioideae and Cypripedioideae. Because of the stamen number and partial column development, the orchids with more than one anther (misleadingly referred to as diandrous) are considered to be more primitive than the monandrous orchids (e.g., Dressler, 1981). The categories within the subfamilies (tribes and subtribes) are based on a variety of characters including vegetative and floral features and habit type. As is true with a number of the flowering plant families, many of the groups (subfamilies, tribes and subtribes) proposed in the various classifications of the orchids are poorly defined and subject to constant rearrangements that appear, at least in some cases, to be merely a matter of intuition.

We have identified 68 apomorphies organized into 42 transformation series. The apomorphies were used to construct a cladogram (Figure 1) from which a classification was developed. The classification presented here recognizes groups that the cladogram indicates to be natural or monophyletic (sensu Hennig, 1966). The characters used to develop the cladogram were those we found to be consistent within the monophyletic groups they are inferred to delimit (in most instances this was the tribal level). The information available on the column structure for members of the Epidendroideae is incomplete, and consequently the resulting classification for that subfamily is somewhat tentative. The classification presented in this paper is compared in Table 1 with those of Dressler (1981), Garay (1972), Schlechter (1970–1984), Vermeulen (1966), Dressler and Dodson (1960), and Rasmussen (1983).

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TABLE 1.—Classification systems of Orchidaceae

Taxonomist	Apostasioideae	Cypripedioideae	Spiranthoideae
Balogh and Funk (1985)	Apostasioideae Neuwiedioideae	Cypripedioideae	Spiranthoideae Cranichideae Prasophylleae Diurideae
Dressler and Dodson (1960)	—	Apostasieae Cypripedieae	—
Vermuelen (1966)	Apostasiaceae	Cypripediaceae	—
Schlechter (1970–1984)	Apostasiaceae	Cypripedioideae Cypripedieae Paphiopedileae Phragmipedieae Selenipedieae	—
Garay (1972)	Apostasioideae	Cypripedioideae	—
Dressler (1981)	Apostasioideae	Cypripedioideae	Spiranthoideae Erythrodeae Cranichideae
Rasmussen (1983)	Apostasiaceae	Cypripediaceae	—

TABLE 1.—*Continued.*

Neottioideae	Orchidoideae	Epidendroideae	Vandoideae
Neottioideae Neottieae Thelymitreae Geoblasteae Pterostylideae	Orchidoideae Diseae Satyrieae Orchideae	Epidendroideae Arethuseae s.s. Vanillieae Gastrodieae Triphoreae Epidendreae Pleurothallis Group Dendrobieae Malaxideae Maxillarieae Vandeae Coelogyneae	—
—	Orchidoideae Neottieae Orchideae Epidendreae	—	—
Epidendroideae Contribe Neottieae	Orchidoideae	Epidendroideae Contribe Epidendranthae	—
Neottioideae Tropideae Neottieae Spirantheae Diurideae	Orchidoideae Satyrieae Orchideae Diseae	Epidendroideae Podochileae Arethuseae, Epidendreae Vandoideae Maxillarieae Oncidieae Cataseteae Vandeae	—
Neottioideae Epipogieae Cranichideae Neottieae	Orchidoideae Orchideae Diseae Disperideae	Epidendroideae Epidendreae Vandeae	—
—	Orchidoideae Diseae Neottieae Diurideae Orchideae	Epidendroideae Epipogieae Vanillieae Gastrodieae Arethuseae Coelogyneae Malaxideae Cryptarrheneae Epidendreae Calypsoeae	Vandoideae Cymbidieae Vandeae Polystachyeae Maxillaireae
Neottioideae Epipactieae Neottieae (= Spiranthoideae and Listerinae)	Orchidoideae Diurideae Orchideae	Epidendroideae Arethuseae Vanilleae Gastrodieae Epipogieae Coelogyneae Malaxideae Epidendreae	Vandoideae Polystachyeae Cymbidieae Maxillarieae Vandeae

advice and criticism. We thank H. Robinson for his encouragement. We thank E. Greenwood, J.B. Comber, and M. Clements for the use of some of their color photos and the following for sending flowers, pollinaria, photos or drawings: P. Bernhardt, M. Clements, J.B. Comber, R.L. Dressler, E. Greenwood, E. Hagsater, H. Kurzweil, J. McQueen, and F.N. Rasmussen. Thanks go to B. Kahn for helping to assemble the manuscript. We also thank the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and the University of Maryland, College Park, Maryland, for supplying SEM time and assistance. Fresh flowers were obtained from the U.S. National Orchid Collection and Marie Selby Botanical Garden.

History of Orchid Classification

John Lindley has aptly been named the father of orchidology. The work that eventually became his book, *The Genera and Species of Orchidaceous Plants* (1830–1840), is the basis on which all modern systems of orchid classification are founded. He divided the approximately 2000 species of orchids then known into seven tribes on the basis of anther number and type of pollinarium. A variation of Lindley's system appeared during the latter part of the 1800s in Bentham (1881). In 1888 and 1889, Pfitzer used vegetative characters as well as column characters to separate the orchids into groups. His major divisions were based on the following: number of anthers, stem and leaf characters, and the consistency of the pollinaria. For many orchidologists his system was not satisfactory because many genera considered to be closely related were put in separate alliances. Later, Rudolf Schlechter (1926) developed a system of classification modified from Pfitzer. Schlechter's system is still used in some major herbaria. His tribes were based on anther and pollinarium characters while the subtribes were based on vegetative and floral characters.

In 1937, Mansfield treated only the monandrous orchids using the methods of both Bentham (1881) and Schlechter (1926), but his groups were basically those of Lindley, although many of the genera had been placed in different groups. Dressler and Dodson (1960) segregated the orchids into tribes and subtribes based on their level of specialization, but the classification still contained the principal groups devised by Lindley.

There are two major conflicts that separate modern orchid systematists. The first difference of opinion concerns the level of recognition of some of the major taxa within the orchids. One group of workers emphasizes the similarities that unite all orchids (partial fusion of the filaments and style, lack of endosperm, mostly resupinate flowers, two inner lateral and one outer median stamen positions) and thinks the Cypripedioideae and Apostasioideae (diandrous and triandrous orchids) should be included in the Orchidaceae (Dressler, 1981; Garay, 1972). A second group of systematists stresses the importance of the differences between the diandrous/triandrous and monandrous orchids and raises one or two of the subfamilies mentioned above to family level (Vermeulen, 1966; Schlechter, 1926, 1970–1984).

The second major disagreement concerns the placement, recognition and contents of the subfamily Neottioideae (Garay, 1972; Polychondreae of Schlechter, 1911). In 1826, Lindley described the Neottieae (sic; = subfamily), which included the tribes Neottieae and Gastrodieae. However, in a later treatment (1830–1840) he dropped the higher category and only recognized the tribe Neottieae, which he characterized by the distinctive dorsal anther and the powdery pollen. Since Lindley's latter work the genera in the Neottieae have been shuffled among the Epidendroideae, Orchidoideae, Spiranthoideae, and Neottioideae. Dressler and Dodson (1960) recognized the Neottieae as a tribe of the Orchidoideae; Vermeulen (1966) recognized them at the contribe level (groups of tribes) and placed them in the Epidendroideae; Schlechter, (1970–1984) and Garay (1972) recognized Neottieae as a distinct subfamily—Neottioideae. Dressler (1981) recognized the significance of anther position when he reorganized and segregated the tribes in Neottioideae. He removed Erythrodeae and Cranichideae, because that group of orchids has inconspicuous staminodia and an erect dorsal anther subequal to the rostellum. He placed these two tribes in a new subfamily, Spiranthoideae. He placed the Diurideae and Neottieae with the Orchideae and the Diseae in the subfamily Orchidoideae because of their terminal erect anther, root-stem tuberoids, lack of stomatal subsidiary cells, and a shared similar habit. Controversy arose when Dressler assumed the Orchidoideae (in the traditional sense) were specialized diurids. The placement of the "neottioid" orchids has received the recent attention of Rasmussen (1982). He suggests that the neottioids are the lowermost branches of the monandrous orchids, i.e., a paraphyletic group, phylogenetically comprising all the other monandrous orchids. In his paper on the Orchidales (1983) Rasmussen does include the Diurideae with Orchidoideae s. s. because of the scattered occurrence of orchidoid characters such as basitony. He regards Diurideae as a remnant group of Orchidoideae.

Objectives of Systematics

The way we "do systematics" is strongly influenced by what we hope to achieve with our systematic studies. Most taxonomic studies have two basic goals: (1) delimiting and identifying taxa, and (2) expressing the inter-relationships among the taxa. The process of achieving these goals can be referred to as developing a classification—certainly a good classification *attains* both these goals. There are different ways of developing a classification and the means one uses dictates the type of information expressed. One can be either intuitive or methodological; the latter procedure can be further expressed as either cladistics or phenetics.

For a number of years orchid systematists have been relying on intuition; practically, this resulted in a combination of character weighting and some type of *Gestalt* evaluation (overall similarity). The taxonomist studied a group of organisms, selected characters she/he believed to be conservative (i.e., important), and delimited the groups of species based on these characters. Disagreements arose when a different taxonomist thought different characters were "more important." If relationships within and among the groups of organisms were expressed, it was usually done with little explanation as to why certain relationships were selected. There have been two recent attempts to develop an empirical method for determining classifications—cladistics and phenetics.

PRINCIPLES OF PHYLOGENETIC SYSTEMATICS

The basis of phylogenetic systematics (Hennig, 1966) is the recognition and maintenance of the phylogenetic relationships among monophyletic groups. The reasoning process works as shown in the following example. Given any three taxa, which two are more closely related to one another than either is to the third? The question is answered by finding an evolutionarily unique character(s) (an apomorphy) in two of the taxa and not in the third. The two that share the unique character are then grouped together. An apomorphy is called synapomorphy if it is shared by two or more taxa, or autapomorphy if it is found in only one taxon. Phylogenetic systematists choose to emphasize the geneological relationship among groups of taxa. We believe it is the best method for developing a classification (Farris, 1983; Nelson and Platnick, 1981). Implementation of the method can be described generally as following these "steps:" select the characters, group them into transformation series, determine which character(s) in each transformation series is (are) apomorphic, group the taxa based on shared apomorphies, and use the resulting cladogram to develop a hierarchial classification.

Hennig used the term phylogenetic systematics for his philosophy. The term cladistics, which was introduced later, is often used in place of phylogenetic systematics. However, as defined by Wiley (1981), cladistics is the method by which the cladogram is constructed and phylogenetic systematics is the entire philosophy of the method. Inherent in phylogenetic systematics are homology, parsimony, and monophylesis.

Homology applies to characters inherited from a common ancestor. The entire character selection process is actually a search for homology. We attempt to put homologous characters into the same transformation series. For instance, we treat the hamular stipe and tegular stipe in two different transformation series because we have evidence from the studies of Rasmussen (1982) that they are structurally different. Of course, characters that appear to be homologous at the beginning of the study may be shown by the cladogram to be more easily explained with a hypothesis of parallel or convergent evolution (homoplasy), appearing two or more times. Concerning the stipe characters mentioned above, both were found at least two times on the cladogram (Figure 1) indicating that neither all of the tegular stipes nor all of the hamular stipes were homologous.

Parsimony (accepting the simplest explanation for the data) is applied on two levels. On the character level it means that within each transformation series we orient the characters with respect to one another in the simplest way possible. This orientation is based on ontogenetic and developmental information for the study group and the characters found in the most closely related groups (outgroups). Those characters present in both the group under study and in the outgroup are said to be the general condition (Platnick, 1979) and are referred to as plesiomorphic (symplesiomorphies are shared general characters). The other characters within the transformation series are all considered to be apomorphic. Transformation series that have more than one apomorphic character are more difficult because it is impossible to tell from outgroup comparison how the apomorphies are related to one another. Because of this difficulty we have chosen to treat such apomorphies as independently derived. One of the more difficult cladistic concepts to explain is that apomorphies are relative. For instance, if we use the lack of endosperm as a synapomorphy for all orchids, then within the family that character is plesiomorphic. Likewise, if the presence of two inner lateral staminodes is a synapomorphy for the monandrous orchids then that character cannot be used to circumscribe groups such as Epidendroideae and Orchidoideae that are contained within the larger group of monandrous orchids. For the cladograms, applying the parsimony principle does not mean that evolution is parsimonious, it means that we seek the diagram that requires the fewest number of assumptions of parallel evolution and reversals (for a detailed explanation see Farris, 1983). Parsimony is the only logical criterion for choosing a cladogram because it gives us the one that best fits the data.

Monophyletic groups are the only ones that are recognized as natural or significant in cladistic classifications. Monophyletic groups are delimited by the presence of an apomorphy. Non-monophyletic groups are not definable by unique characters and have not had a unique history in common. Certainly non-monophyletic groups do not contain all of the descendants of an ancestor and are, therefore, not natural groups.

Additional explanations on the above topics accompany the various sections of this study and can be found in the following references: Eldredge and Cracraft (1980), Nelson and Platnick (1981), and Wiley (1981).

We will first examine intuitive and phenetic classifications of orchids before presenting our cladistic classification. Previous to this study only a few cladistic studies of orchid genera have been published: *Brownlea* (Linder, 1981a), *Monadenia* (Linder, 1981b), *Hershelia* (Linder, 1981c), and the Neottioid orchids (Rasmussen, 1982).

TRADITIONAL ORCHID SYSTEMATICS

Orchid taxonomy is fraught with the classic problems of intuitive or *Gestalt* systematics. The problems, which fall into a number of somewhat overlapping categories, include: the use of inconsistent characters, grouping by plesiomorphies, circular reasoning, intuition (used when there is a lack of data), appeal to authority, character weighting, overall similarity (phenetics), and the use of groups of characters as characters (a few examples are given below and additional discussion can be found throughout this paper).

In 1981, Dressler used three characters to delimit the subfamily Orchidoideae: presence of root-stem tuberoids, lack of stomatal subsidary cells, and an erect anther. While Dressler placed all taxa that have root-stem tuberoids into the Orchidoideae, he also included taxa that did not have them, and in fact, this character is usually consistent only at the generic level. For instance, Rasmussen (pers. comm., 1983) reports that not all Diurideae, which supposedly have root-stem tuberoids, actually have this type of structure. His preliminary studies indicate this structure is only a swollen root without the polystelar root-stem tuberoid anatomy. The root stem tuberoid is absent in the Neottieae and is inconsistent as a character in the Orchideae.

The erect anther is the plesiomorphic character (see "Discussion of Characters as Displayed on the Cladogram," p. 41) giving rise to three different anther types: upside-down, at right angles to the column axis, and operculate-incumbent. The presence or absence of subsidiary cells is a very inadequately studied character (Rasmussen, 1982) and so much missing data limits its usefulness. While each of the three apomorphic characters can be used to group taxa, the retention of the plesiomorphic character gives us no information on relationship. Dressler's Orchidoideae contains taxa with different column morphologies. He evidently considers the three characters listed above, two of which lack conclusive data, as more important; this is character weighting.

Garay (1972) gives very little explanation as to why he groups certain things together in his classification, he simply presents it. This is a classic example of "appeal to authority" because we are asked to accept the classification because of expertise in the field, not because of data presented. Intuition and overall similarity work in much the same manner. Workers will cite *Gestalt* as a reason for separating taxa, or will discuss how different the subtribes are, but will not be able to list the characters they used to differentiate them.

Apostasia and *Neuwiedia* are usually grouped together because they are primitive, and certain characters, such as partial fusion of the androecium and gynoecium, are considered primitive because they are found in these two genera. The fact remains, however, that many workers do not regard them as closely related (Garay, 1972). Garay stated that "*Apostasia* and *Neuwiedia* are not even closely related to one another but are only relic survivors of ancient anagenetic lines." This is a fine example of circular reasoning. Why are the genera primitive? Because they have primitive characters. Why are the characters primitive? Because they are found in primitive groups. Actually we found that the two genera were not particularly closely related and that like all other taxa, both have some apomorphic and well as plesiomorphic characters. Another example of circular reasoning is found in Garay (1960). He regards the heavy sclerotic seed coat in *Vanilla* as a primitive character because *Apostasia nuda* and *Selenipedium chica* have a similar type of seed. A character is not primitive because it is found in a primitive group. Our results agree with those of Rasmussen (1983); the sclerotic seed coat is more likely secondarily derived.

Often taxonomists will use characters that are really groups of characters; a good example in orchids is habit. Orchids are epiphytic, terrestrial, autotrophic, or saprophytic; much discussion takes place about which of these habits is primitive (Benzing, 1981). The habit is not a character. What are characters are the features that enable the plant to have one of the three habits, such as the presence or absence of velamen in the roots, or small seeds (Robinson and Burns-Balogh, 1982).

Phenetics and Orchid Classification

Others have noted the various problems with traditional classification and have attempted to be more empirical in their studies. The various phenetic approaches concentrate on reflecting the total similarity of the organisms in question. In practice this means that given any three taxa the two that appear more similar to one another are grouped together. Lavarack completed a dissertation exploring the relationships within the Neottioideae (1971, unseen) and published two papers summarizing his work (1974, 1976). He concentrated on the Australian taxa but the analysis included members of all of the subfamilies. In his 1976 paper he seeks to "consider relationships as indicated by an examination of overall similarity." This type of study involves using all possible characters and evaluating the relationships using a variety of computer programs that use different algorithms (for a detailed discussion of the advantages and disadvantages of these programs see Sneath and Sokal, 1973). Although Lavarack used a few column characters for his published studies, he relied mainly on vegetative characters.

Phenetic studies eliminate some of the problems of intuitive classification discussed above, such as circular reasoning, intuition, appeal to authority, and groups of characters. Other problems are retained, however, though sometimes in a different manner. For example, phenetic studies of orchids deal only with individuals and can therefore use characters that are known to vary within the group as a whole. For instance, one character in Lavarack's study is the "number of leaves" and this is divided into three states (none, one, and more than one). In the genera *Cattleya* (Epidendreae) and *Spiranthes* (Cranichideae) two or more states are known to occur; this is also the case with several other genera in his study. In Lavarack's character of the leaf bases, one is not sure what he means, but within the genus *Spiranthes* (Spiranthoideae) several different types of leaf base occur. Another of Lavarack's characters, ovate versus linear leaves, has both states often found in the same genus. Still another example, the length of the column, is so variable that it cannot be used on the subtribal level (e.g., Spiranthinae, Balogh, 1982). We could go on, but the point is obvious. By looking at only one individual or species one can make a judgement; the information that the character varies is either ignored or considered to be unimportant.

Because phenetic studies treat all characters equally, they group by plesiomorphies as well as apomorphies (see discussion of traditional orchid systematics). Character weighting occurs, however, because of the various ways of coding multistate characters. Also, because there is no need to thoroughly examine the distribution and morphology of the characters in order to decide on homology and polarity, some characters are really groups of characters.

Phenetics has the additional problem of dividing characters into "character states," which are then treated as distinct entities rather than sets and subsets. An example from orchids is the number of chambers in the ovary. Figure 2 shows the difference between treating characters as having states and treating them as internested. In the Orchidaceae the ovary can be either three-chambered or one-chambered. In a phenetic study these are treated as two distinct states of the same character and both can be used to group taxa. So, the use of "character states" is tied directly to the procedure of grouping with plesiomorphic characters because when "character states" are discrete entities they can be given equal value in grouping. Cladistically, the one- and three-chambered ovaries are treated as nested. This is easiest to see using a Venn diagram (Figure 2). The three-chambered ovary character is plesiomorphic and the one-chambered is apomorhic (evolutionarily novel). The one-chambered ovary is treated as a subset of the three-chambered one and all taxa that have the apomorphy are also considered to have the three-chambered ovary because one has developed from the other. After the cladogram was completed it was best to hypothesize that the development of the one-chambered ovary had occurred twice in the Orchidaceae.

In addition to the procedural difficulties, we find the results of phenetic studies irritating because we are presented with a diagram, but have no way of knowing which characters are responsible for the various branches (this is also a problem with some intuitive trees).

Interestingly the written classification from Lavarack's study does not strictly follow the groups indicated in the dendrograms. Rather, it shifts genera around when the results are undesirable. In Lavarack's own words (1976, p. 293):

> This classification does not follow exactly the results presented in Figures 1 and 2 but is a composite of those results, the results of other analysis only briefly discussed here, and the personal ideas and prejudices of the author.

It all sounds rather like traditional intuitive systematics. It seems then, that as applied in the Orchidaceae, phenetics has not only many of the problems of traditional systematics but a few additional problems as well.

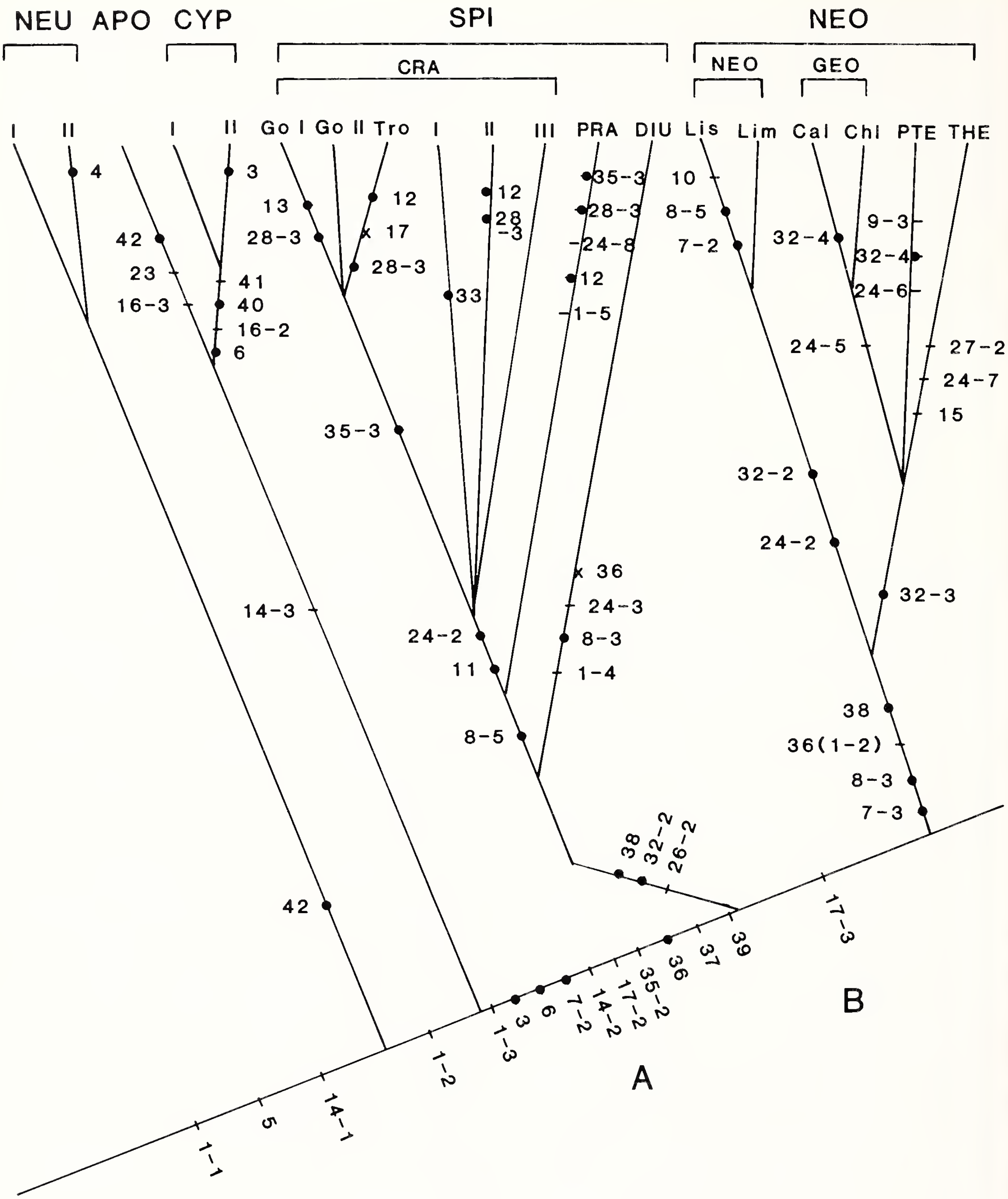
Cladistic Analysis of the Orchidaceae

Character Selection

Decisions on polarity of characters are based on the outgroup comparison method (Hennig, 1966; Platnick, 1979; Watrous and Wheeler, 1981), in which the more general characters are plesiomorphic. The character designated by the lowest number (1) is the most plesiomorphic one for each transformation series (Table 2).

All characters, both floral and vegetative, were considered in this study. Only characters that proved to be consistent were used in the cladistic analysis, however. Consistent characters are those that do not vary within the study taxa. For our purposes that meant that the characters had to be consistent at the tribal level. Exceptions at the species level are not treated in this cladistic analysis and are only mentioned under the subtribal descriptions. We consider these exceptions to be apomorphies at the species or generic level. Some of the characters were consistent in all of the tribes except for one or two. The tribes where the character was inconsistent were then broken down to subtribes for this analysis. The only exceptions to this were in the size of the pollen unit, i.e., monad or tetrad transformation (series 36), and in the cobra-hood-like inner lateral staminode development (character 24-9). The presence of tetrads varied so much in the Neottioideae that it could not be used even at the subtribal level. It was consistent for the other tribes, however, so we retained it in the analysis and simply listed it as variable for the Neottioideae. Some Epidendroideae have the inner lateral staminodes completely fused to the column structure (character 24-4) and some have them fused to the column margins and cobra-hood-like above the anther (character 24-9). While these characters were consistent on the genus level they were variable on the tribal level and so are listed as both on the cladogram (Figure 1, Area E).

The following transformation series are discussed in the order of their occurrence on the anther and column (for a listing of the characters by number see Table 2). In the remainder of this paper, unless otherwise specified, all subfamilies, tribes and subtribes are those recognized by Burns-Balogh and Funk; a synopsis of these appears at the end of this section (see "Classification of the Orchidaceae" p. 60, for a complete listing). The 68 apomorphic characters are grouped into 42 transformation series (14 transformation series contain more than one apomorphic character). The characters fall into three groups, those dealing with the pistil, with the stamen(s), and with the pollinia. Only a brief description of the characters is possible in this paper. A more de-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32-4
24-6
24-5
27-2
24-7
15
35-3
32-2
24-2
32-3
14-3
24-2
11
8-5
36
24-3
8-3
1-4
38
36(1-2)
8-3
7-3
38
32-2
26-2
42
3
6
7-2
14-2
17-2
35-2
36
37
39
17-3
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1-2
14-1
5
1-1
A
B

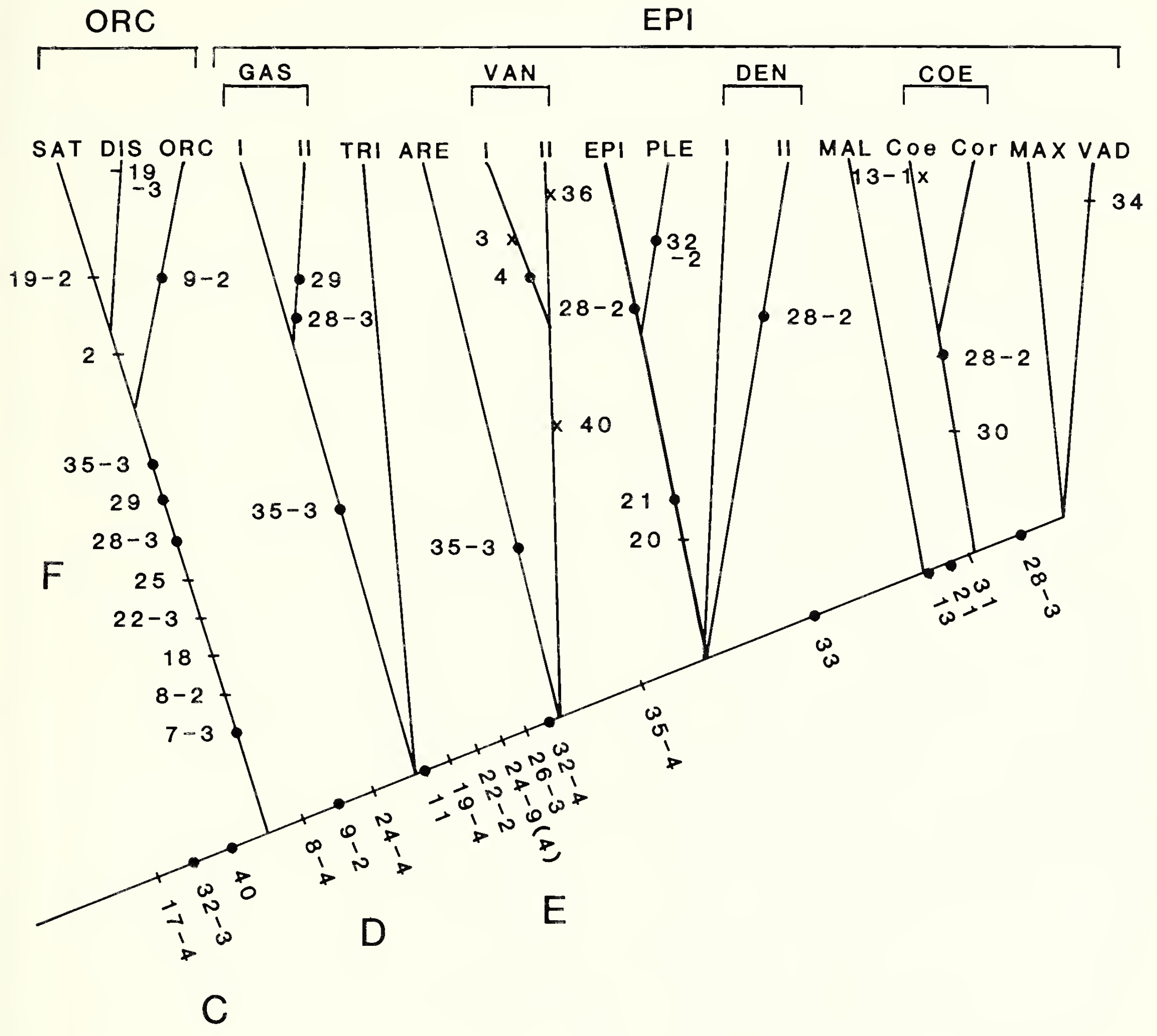

FIGURE 1.—Cladogram of the Orchidaceae. Lines = synapomorphies, closed circles = homoplasies (parallel or convergent evolution), x = loss of a synapomorphy (reversal). **NEU** = Neuwiedioideae; **APO** = Apostasioideae; **CYP** = Cypripedioideae; **SPI** = Spiranthoideae, CRA = Cranichideae, Go = Goodyerinae, Tro = Tropidinae, PRA = Prasophylleae, DIU = Diurideae; **NEO** = Neottioideae, NEO = Neottieae, Lis = Listerinae, Lim = Limodorinae, GEO = Geoblasteae, Cal = Caladeniinae, Chl = Chloraeinae, PTE = Pterostylideae, THE = Thelymitreae; **ORC** = Orchidoideae, DIS = Diseae, SAT = Satyrieae, ORC = Orchideae; **EPI** = Epidendroideae, GAS = Gastrodieae, TRI = Triphoreae, ARE = Arethuseae, VAN = Vanilleae, EPI = Epidendreae, PLE = Pleurothallis group, DEN = Dendrobieae, MAL = Malaxideae, COE = Coelogyneae, Coe = Coelogyninae, Cor = Corallorhizinae, MAX = Maxillarieae, VAD = Vandeae. Data matrix for this cladogram is in Table 3. Constancy index = 60%. Numbers listed are found in Table 2. A–F = areas of the cladogram referred to in the "Discussion" (see page 41).

TABLE 2.—Characters and their respective transformation series used in the "Cladistic Analysis of the Orchidacae."

Transformation series	Character
Pistil	
1. Fusion of style	0. free 1. style fused w/filaments at bases 2. style fused w/filaments and staminode bases 3. style fused w/ filaments, staminodes, and stigma to column 4. style extremely reduced or absent 5. style fused w/filament and staminode bases, style reduced
2. Bending of style	1. erect or bending forward 2. bending backward
3. Ovary chambers	1. 3-chambered 2. 1-chambered
4. Fruit type	1. capsule 2. berry
5. Endosperm	1. present 2. absent
6. Stigma modification	1. none or slightly asymmetric 2. all lobes facing toward center of flower
7. Viscidium attachment on pollinia	1. no viscidium 2. at or near apex 3. at or near base
8. Rostellum (modified portion of median stigma lobe) shape	1. all three stigma lobes identical or slightly asymmetrical; no rostellum 2. rostellum strap-like, between bases of anther theca 3. rostellum highly reduced 4. rostellum curled over and as long as wide or wider 5. rostellum longer than wide
9. Stigma	1. slightly convex 2. concave 3. very oblong, extending ¼–¾ of the way down column
10. Rostellum	1. not sensitive 2. sensitive
11. Clinandrium fusion	1. incomplete 2. complete
12. Hamulus stipe	1. absent 2. present
13. Tegular stipe	1. absent 2. present
Stamen	
14. Number	1. one outer median and two inner laterals 2. outer median 3. inner laterals
Median Outer Stamen	
15. Fusion of entire filament only with staminodes	1. no 2. yes
16. Outer median staminode	1. none (still an anther) 2. well developed 3. filament-like
17. Anther base position (insertion on filament)	1. below stigma 2. at or near stigma base, anther rarely extending beyond rostellum 3. at or near stigma apex (lateral lobes), anther extending above rostellum 4. above stigma apex (lateral lobes), anther extending above rostellum
18. Fusion of outer median anther base to column apex	1. free 2. fused
19. Development of outer-median stamen in relation to column axis	1. erect to suberect 2. up-side-down 3. at right angles to column axis 4. operculate, incumbent to hyperincumbent
20. Locules	1. rarely more than 4 2. 2 to 12
21. Anther condition	1. never deciduous 2. deciduous (not always)
22. Anther modification	1. lily-like 2. cap-like 3. bases of thecae usually separated, often widely

TABLE 2.—*Continued.*

Transformation series	Character
Inner Lateral Stamens	
23. Anther tube (adherent margins of stamens and if present, margins of staminode) surrounding style	1. absent 2. present
24. Inner lateral staminode development	1. none (still anthers) 2. fused to style for most of length but apices free and projecting, often inconspicuous 3. long membranous 4. not apparent, completely fused to column structure 5. fused to margins of column and flared at apex, cobra-hood-like below anther 6. fused to margins of column, broad and hook-like at upper ⅓–½ 7. hood-like surrounding stigma and anther, with pseudostamens or other ornamentations 8. long and thick 9. fused to column margins and cobra-hood-like above anther, margins of staminodes fused to each other at apex and behind or above anther
25. Auricles	1. absent 2. present
26. Clinandrium composition	1. absent 2. back of stigma and staminode margins 3. back of rostellum and probably staminode margins
27. Staminode to staminode fusion	1. free from each other but fused to column at some point, sometimes only at the very apex 2. inner margins fused forming a hood-like structure
Pollinia	
28. Caudicle composition	1. none 2. embedded with pollen 3. sterile; just elastoviscin
29. Caudicle length	1. short, reduced, connective 2. tail-like, elongate
30. Caudicle to caudicle fusion	1. free 2. fused
31. Pollinia position	1. side by side 2. superposed
32. Pollinia shape	1. unformed 2. attenuate apex, rounded base 3. rounded apex, attenuate base 4. rounded apex and base
33. Pollinium set size	1. each member +/− equal 2. unequal
34. Pollinium fusion	1. free 2. fused to each other in set
35. Pollen aggregation	1. powdery, non-aggregated, or sticky 2. granulate, consolidated 3. sectile 4. hard, waxy
36. Pollen unit	1. monad 2. tetrad
37. Elastoviscin	1. absent 2. present
38. Cohesion strands	1. absent 2. present
39. Aperture	1. colpate 2. porate/ulcerate
40. Foot layer	1. present 2. absent
41. Incipient columellae	1. absent 2. present
42. Operculate culpus	1. absent 2. present

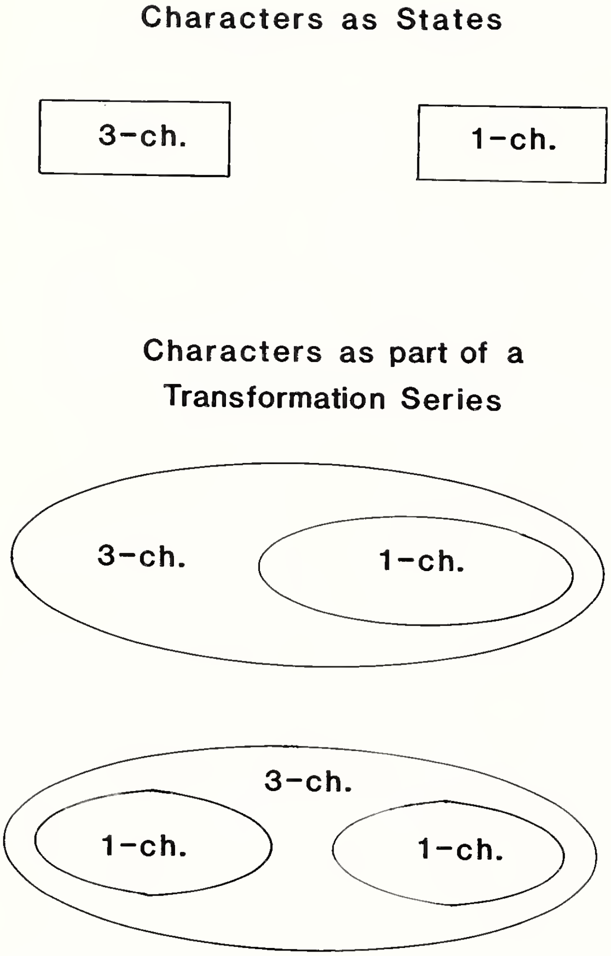

FIGURE 2.—Characters as character states and as members of a transformation series. This example treats single-chambered vs. 3-chambered ovaries.

tailed discussion of the characters used in this analysis can be found in a series of papers published in the *Orchid Review* (Burns-Balogh, 1983a, b; Burns-Balogh and Funk, 1983) and *The Canadian Orchid Journal* (Burns-Balogh, 1984a, b; Burns-Balogh, Borg-Karlson, and Kullenberg, 1985). We are not prepared to say which family is most closely related to the Orchidaceae but it is undoubtably something in the Liliales, so for most characters we used the entire subclass as the outgroup in this study. The Appendix contains a list of all specimens examined and Table 3 has the data matrix used in this analysis.

Synopsis of Burns-Balogh and Funk Classification

- Neuwiedioideae
- Apostasioideae
- Cypripedioideae
- Spiranthoideae
  - Diurideae
  - Prasophylleae
  - Cranichideae: Cranichidinae, Spiranthinae, Manniellinae, Cryptostylidinae, Pachyplectroninae, Tropidiinae, Goodyerinae*
- Neottioideae
  - Geoblasteae: Caladeninae, Chloraeinae*
  - Pterostylideae
  - Thelymitreae
  - Neottieae: Listerinae, Limodorinae* (including Rhizanthellinae)
- Orchidoideae
  - Orchideae: Orchidinae, Habenariinae, Huttonaeinae
  - Diseae: Diseae, Coryciinae
  - Satyrieae
- Epidendroideae
  - Gastrodieae: Gastrodiinae, Epipogiinae, Stereosandrinae(?), Wullschlaegeliinae(?), Nervilinae
  - Triphoreae*: Tropidieae, Acianthinae(?)
  - Arethuseae
  - Vanilleae: Vanilliinae, Pogoniinae, Palmorchidinae, Lecanorchidinae
  - Dendrobieae*: Thuniinae, Glomerinae, Dendrobiinae, Bulbophyllinae, Sunipiinae
  - *Pleurothallis* Group: Pleurothallidinae, Meiracyllinae, Thelasinae, Podochilinae, Eriinae, Adrorhizinae
  - Epidendreae: Laeliinae, Bletiinae, Sobralinae
  - Malaxideae*
  - Coelogyneae: Corallorhizinae*, Coelogyninae
  - Maxillarieae*: Zygopetalinae, Bifrenariinae, Lycastinae, Maxillariinae, Dichaeinae, Telipoginae, Ornithocephalinae, Polystachyinae, Cryptarrheninae, Calypsoinae
  - Vandeae: Sarcanthinae, Aerangidinae, Angraecinae, Eulophiinae, Cyrtopodiinae, Genyorchidinae, Acriopsidinae, Catasetinae, Stanhopaeinae, Thecostelinae, Onciinae, Pachyphyllinae

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* Not indicated to be monophyletic groups.

FIGURES 3–36.—Column morphology of the Orchidaceae. Key to letter symbols: A = anther, S = stigma, ST = staminode, V = viscidium, R = rostellum, C = column, AU = auricle, CL = clinandrium. Line length = 5 mm except in Figure 9, where line length = 1 mm.

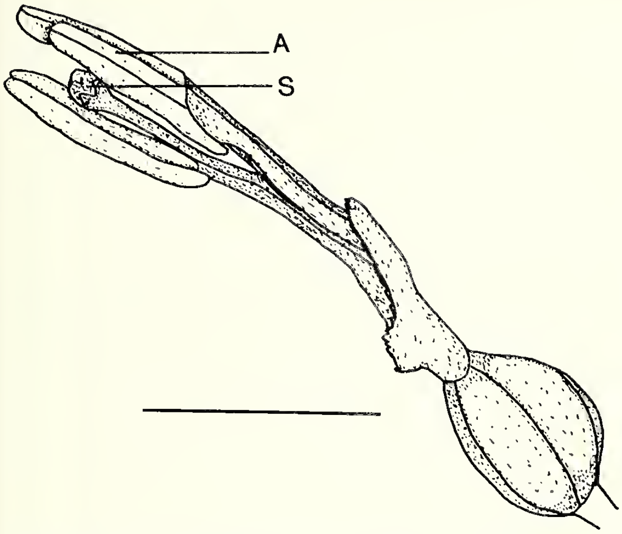


FIGURE 3.—Neuwiedioideae, *Neuwiedia singapureana* (Baker) Rolfe. Booea 25570 (US).

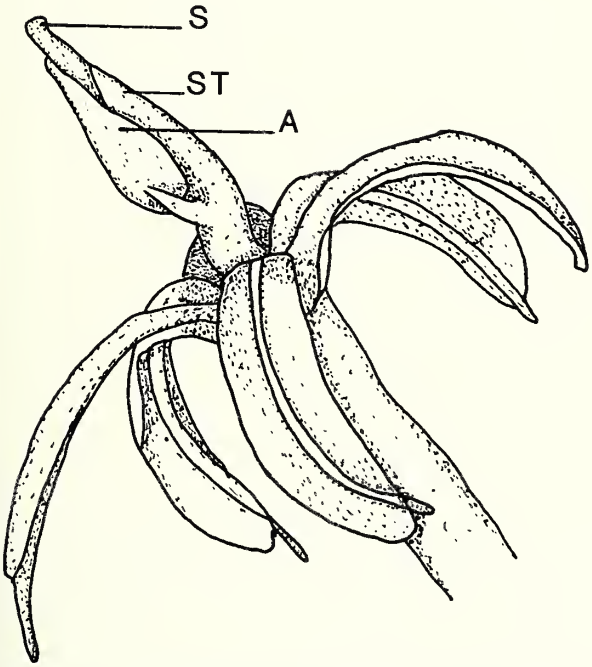


FIGURE 4.—Apostasioideae, *Apostasia wallachii* R. Brown ex Wallich. Dressler s.n. (from photo).

Discussion of Characters and Their Aggregation into Transformation Series

CHARACTERS OF THE PISTIL

In many orchids, most of the bulk of the column structure is composed of the style. In transformation series 1 (t.s. 1), the fusion of the style with the various structures results in the formation of the column. The basic condition is found in Neuwiedioideae (Figure 3), which is most similar to other Lilidae with only basal fusion of style and filaments, while the diandrous orchids (Figures 4–6) have a "column" formed by the fusion of the filaments, staminode base, and style (Plate 3*a*). The monandrous orchids, on the other hand, have a complete column structure (Figures 7–36) resulting from the fusion of the style, stigma, staminodes, the filament of the fertile anther, and in some cases, i.e., the Orchidoideae, the anther base (Plate 3*d–f, h–i, k–n*, Plate 4*b–d, f–i, k*). In the Diurideae, reduction in the above structures has resulted in the "absence" of a column structure (Figure 10) while in Prasophyllinae (Figure 11) the column is very reduced and composed of only the bases of the filament, style, stigma, and staminodes. The style is usually erect or bending forward (Table 2, t.s. 2), but in Diseae (Figure 21) and Satyrieae (Figure 22) the bending at the apex of the column results in a reversal in the position of the anther (and stigma in Satyrieae).

Compared to the other families in the monocotyledons the pistil has undergone great modification, including the following: reduction in the number of ovary chambers (Table 2, t.s. 3); lack of an endosperm (Table 2, t.s. 5); all three or two lobes present on one side of the gynoecial apex facing the center of the flower (Table 2, t.s. 6); and the formation of the rostellum from the median stigma lobe (Table 2, t.s. 8). The possession of three functional stigmatic lobes is the general condition found in the monocotyledons and is therefore considered to be plesiomorphic

TABLE 3.—Data matrix; number of characters per transformation series in all transformation series with more than two characters each apomorphy was treated independently of the others and no sequential relationship was inferred until after the cladogram was constructed (B = both).

TAXA/TS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
NEU I	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NEU II	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
APO	2	1	1	1	2	1	1	1	1	1	1	1	1	3	1	3	1	1	1	1
CYP I	2	1	1	1	2	2	1	1	1	1	1	1	1	3	1	2	1	1	1	1
CYP II	2	1	2	1	2	2	1	1	1	1	1	1	1	3	1	2	1	1	1	1
Go I	3	1	2	1	2	2	2	5	1	1	2	1	2	2	1	1	2	1	1	1
Go II	3	1	2	1	2	2	2	5	1	1	2	1	1	2	1	1	2	1	1	1
Tro	3	1	2	1	2	2	2	5	1	1	2	2	1	2	1	1	1	1	1	1
Tro I	3	1	2	1	2	2	2	5	1	1	2	1	1	2	1	1	2	1	1	1
Tro II	3	1	2	1	2	2	2	5	1	1	2	2	1	2	1	1	2	1	1	1
Tro III	3	1	2	1	2	2	2	5	1	1	2	1	1	2	1	1	2	1	1	1
PRA	5	1	2	1	2	2	2	5	1	1	1	2	1	2	1	1	2	1	1	1
DIU	4	1	2	1	2	2	2	3	1	1	1	1	1	2	1	1	2	1	1	1
Lis	3	1	2	1	2	2	3	4	1	2	1	1	1	2	1	1	3	1	1	1
Lim	3	1	2	1	2	2	3	3	1	1	1	1	1	2	1	1	3	1	1	1
Cal	3	1	2	1	2	2	3	3	1	1	1	1	1	2	1	1	3	1	1	1
Chl	3	1	2	1	2	2	3	3	1	1	1	1	1	2	1	1	3	1	1	1
PTE	3	1	2	1	2	2	3	3	1	1	1	1	1	2	1	1	3	1	1	1
THE	3	1	2	1	2	2	3	3	1	1	1	1	1	2	2	1	3	1	1	1
SAT	3	2	2	1	2	2	3	2	1	1	1	1	1	2	1	1	4	2	2	1
DIS	3	2	2	1	2	2	3	2	1	1	1	1	1	2	1	1	4	2	3	1
ORC	3	1	2	1	2	2	3	2	2	1	1	1	1	2	1	1	4	2	1	1
GAS I	3	1	2	1	2	2	2	4	2	1	1	1	1	2	1	1	4	1	1	1
GAS II	3	1	2	1	2	2	2	4	2	1	1	1	1	2	1	1	4	1	1	1
TRI	3	1	2	1	2	2	2	4	2	1	1	1	1	2	1	1	4	1	1	1
ARE	3	1	2	1	2	2	2	4	2	1	2	1	1	2	1	1	4	1	1	1
VAN I	3	1	1	2	2	2	2	4	2	1	2	1	1	2	1	1	4	1	1	1
VAN II	3	1	2	1	2	2	2	4	2	1	2	1	1	2	1	1	4	1	1	1
EPI	3	1	2	1	2	2	2	4	2	1	2	1	1	2	1	1	4	1	1	2
PLE	3	1	2	1	2	2	2	4	2	1	2	1	1	2	1	1	4	1	1	2
DEN I	3	1	2	1	2	2	2	4	2	1	2	1	1	2	1	1	4	1	1	1
DEN II	3	1	2	1	2	2	2	4	2	1	2	1	1	2	1	1	4	1	1	1
MAL	3	1	2	1	2	2	2	4	2	1	2	1	1	2	1	1	4	1	1	1
Coe	3	1	2	1	2	2	2	4	2	1	2	1	2	2	1	1	4	1	1	1
Cor	3	1	2	1	2	2	2	4	2	1	2	1	2	2	1	1	4	1	1	1
MAX	3	1	2	1	2	2	2	4	2	1	2	1	2	2	1	1	4	1	1	1
VAD	3	1	2	1	2	2	2	4	2	1	2	1	2	2	1	1	4	1	1	1

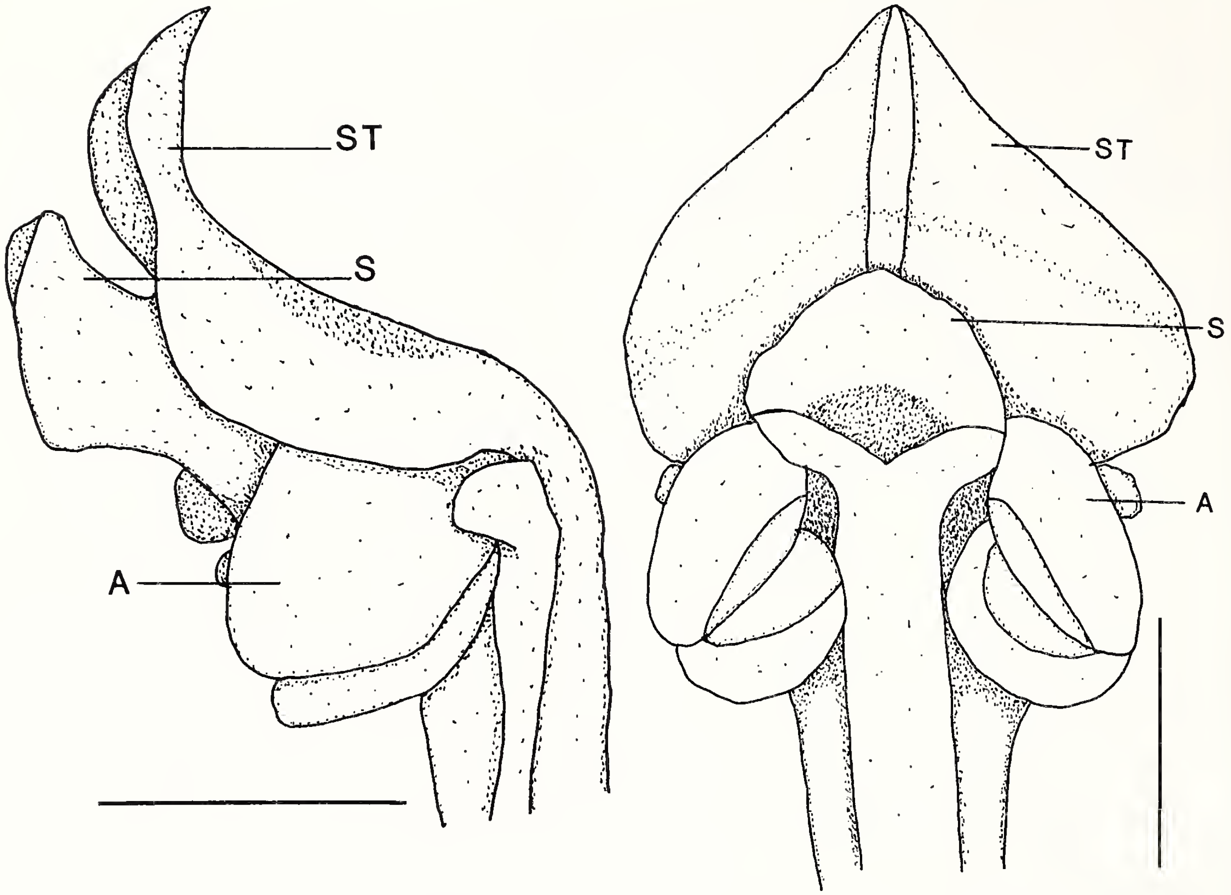
in those orchid genera possessing three functional lobes, such as the triandrous and diandrous orchids plus isolated monandrous orchids such as *Cephalanthera* and perhaps *Rhizanthella*.

The rostellum separates the pollen masses from the functionally receptive stigmatic lobes, supports the pollinarium (until removal by the pollinator), and provides the sticky material or viscidium (by which the pollinia are attached to the pollinator). In some genera where a rostellum or viscidium is lacking, the stigmatic surface may provide the sticky substance. An example of this is *Cephalanthera*. In this paper, the viscidium is treated in the broad sense, i.e., any substance

TABLE 3.—*Continued.*

21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1
1	1	1	2	1	2	1	3	1	1	1	2	1	1	3	2	2	2	2	1	1	1
1	1	1	2	1	2	1	1	1	1	1	2	1	1	3	2	2	2	2	1	1	1
1	1	1	2	1	2	1	3	1	1	1	2	1	1	3	2	2	2	2	1	1	1
1	1	1	2	1	2	1	1	1	1	1	2	2	1	2	2	2	2	2	1	1	1
1	1	1	2	1	2	1	3	1	1	1	2	1	1	2	2	2	2	2	1	1	1
1	1	1	2	1	2	1	1	1	1	1	2	1	1	2	2	2	2	2	1	1	1
1	1	1	8	1	2	1	3	1	1	1	2	1	1	3	2	2	2	2	1	1	1
1	1	1	3	1	2	1	1	1	1	1	2	1	1	2	1	2	2	2	1	1	1
1	1	1	2	1	1	1	1	1	1	1	2	1	1	2	B	2	2	2	1	1	1
1	1	1	2	1	1	1	1	1	1	1	2	1	1	2	B	2	2	2	1	1	1
1	1	1	5	1	1	1	1	1	1	1	4	1	1	2	B	2	2	2	1	1	1
1	1	1	5	1	1	1	1	1	1	1	3	1	1	2	B	2	2	2	1	1	1
1	1	1	6	1	1	1	1	1	1	1	4	1	1	2	B	2	2	2	1	1	1
1	1	1	7	1	1	2	1	1	1	1	3	1	1	2	B	2	2	2	1	1	1
1	3	1	1	2	1	1	3	2	1	1	3	1	1	3	2	2	1	2	2	1	1
1	3	1	1	2	1	1	3	2	1	1	3	1	1	3	2	2	1	2	2	1	1
1	3	1	1	2	1	1	3	2	1	1	3	1	1	3	2	2	1	2	2	1	1
1	1	1	4	1	1	1	1	1	1	1	3	1	1	3	2	2	1	2	2	1	1
1	1	1	4	1	1	1	3	2	1	1	3	1	1	3	2	2	1	2	2	1	1
1	1	1	4	1	1	1	1	1	1	1	3	1	1	2	2	2	1	2	2	1	1
1	2	1	9	1	3	1	1	1	1	1	4	1	1	3	2	2	1	2	2	1	1
1	2	1	9	1	3	1	1	1	1	1	4	1	1	2	2	2	1	2	1	1	1
1	2	1	9	1	3	1	1	1	1	1	4	1	1	2	1	2	1	2	1	1	1
2	2	1	9	1	3	1	2	1	1	1	4	1	1	4	2	2	1	2	2	1	1
2	2	1	9	1	3	1	1	1	1	1	2	1	1	4	2	2	1	2	2	1	1
1	2	1	9	1	3	1	1	1	1	1	4	1	1	4	2	2	1	2	2	1	1
1	2	1	9	1	3	1	2	1	1	1	4	1	1	4	2	2	1	2	2	1	1
1	2	1	9	1	3	1	1	1	1	1	4	2	1	4	2	2	1	2	2	1	1
2	2	1	9	1	3	1	2	1	2	2	4	2	1	4	2	2	1	2	2	1	1
2	2	1	9	1	3	1	2	1	2	2	4	2	1	4	2	2	1	2	2	1	1
2	2	1	9	1	3	1	3	1	1	2	4	2	1	4	2	2	1	2	2	1	1
2	2	1	9	1	3	1	3	1	1	2	4	2	2	4	2	2	1	2	2	1	1

originating from the rostellum which serves to attach the pollen masses to the pollinator. In some cases, e.g., Laeliinae, the viscidium is a viscid fluid and Dressler (pers. comm., 1982) suggests the term "rostellar glue" to distinguish it from the solid viscidium that is usually found in the orchids. The rostellum assumes a variety of shapes and sizes that are represented by the five apomorphic characters (Table 2, t.s. 8). These are treated independently from one another (Table 4). In those orchids with a well-defined rostellum, the viscidium abscisses from the rostellum proper at the time of removal of the pollinia and is considered a part of the polli-

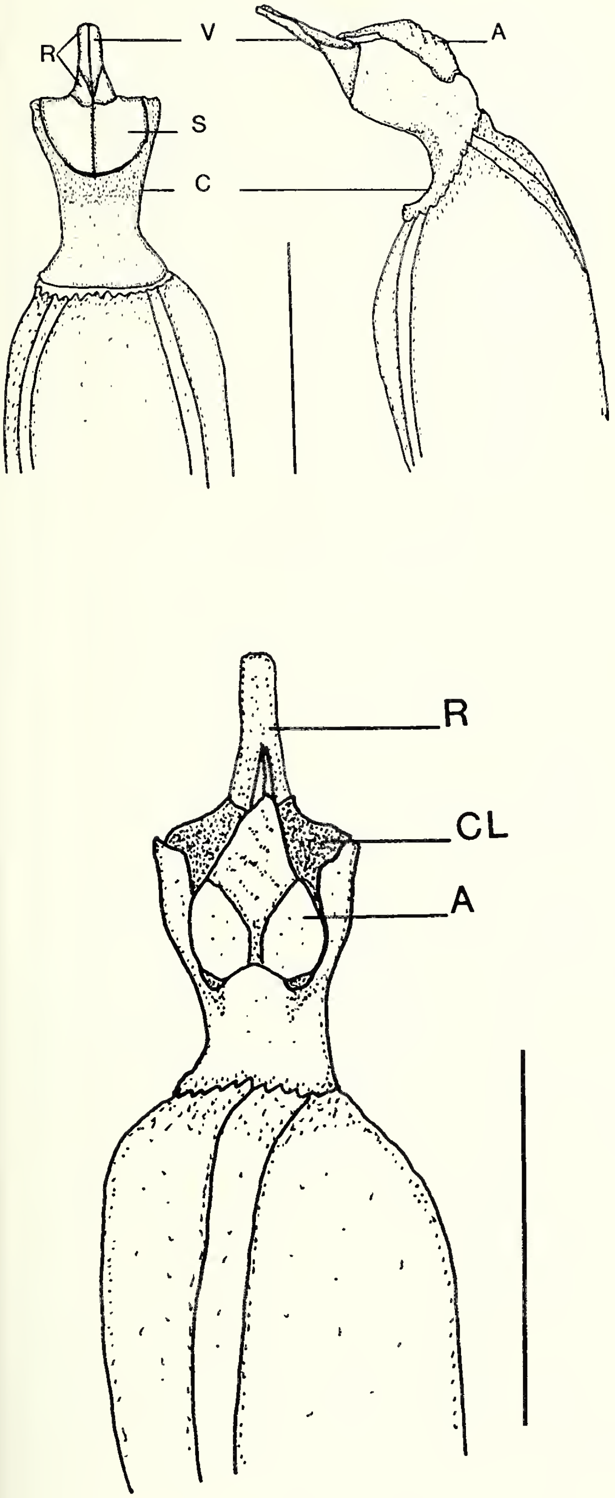


FIGURES 5, 6.—Cypripedioideae, *Cypripedium acaule* Aiton. Balogh 1053 (US).

narium. In some taxa the rostellum is highly reduced (Neottioids) and is usually all viscidium. Consequently, it is almost totally removed with the pollinia. In Listerinae, the rostellum is sensitive to pressure (Table 2, t.s. 10) and exudes a viscid droplet when an insect touches it (the rostellum).

Other apomorphies of the rostellum include the attachment of the viscidium on the pollinia (Table 2, t.s. 7). It may be either apical or at or near the base of the pollinia. Sometimes a portion of the rostellum called a stipe is removed with the pollinarium. Rasmussen (1982) distinguishes between the tegular stipe (modified rostellar epidermis) of the vandoid orchids and some Goodyerinae (Table 2, t.s. 13) and the hamular stipe (recurved apex of the rostellum) of the Prasophyllinae, some Cranichidinae, and Tropidinae, two anomalous genera, *Genoplesium* and *Microtis*, now recognized as members of Neottioideae, and at least one species of *Bulbophyllum* of Dendrobieae/Epidendroideae (Table 2, t.s. 12). Because these two types of stipe are anatomically different we have treated them as different (Table 2, t.s. 12, 13; for illustrations of t.s. 7, 12, and 13 see section on pollinaria, p. 30).

The presence of a clinandrium is apomorphic (Table 2, t.s. 11). There are two types: complete, where the margins of the stigma or rostellum are fused to the margins of the staminodes (often with a short free apex present) (Figure 8); and incomplete, where there is no fusion between the margins of the stigma and staminodes. These two apomorphies are treated independently of one



Figures 7, 8.—Spiranthoideae, Cranichideae, *Spiranthes cernua* (L.). L.C. Rich. Balogh 914 (US).

another.

Other modifications of the pistil include the reduction in the number of the ovary chambers (Table 2, t.s. 3), a berry fruit (Table 2, t.s. 4), and the stigmatic surface that is concave or oblong (Table 2, t.s. 9). The Orchidoideae, Apostasioideae, Neuwiedioideae, two genera in the Cypripedioideae, and a few genera in the Vanilleae, have a plesiomorphic three-chambered ovary. All other orchids have a single chambered ovary. In a few species of *Neuwiedia* and Vanilleae the fruit type is a berry, whereas in all other orchids a capsule is found. The stigmatic surface is sometimes slightly convex. Because this is the condition found in the monocots we have designated it the plesiomorphic character. The apomorphic character of this transition series is the concave surface found in some of the Orchidoideae and in Epidendroideae. In Epidendroideae the concave stigmatic surface is tucked under the roof-like rostellum. This is, in large part, the result of the bending of the column. In the Pterostylideae the stigmatic surface is oblong and extends from approximately ¼ to ¾ down the column to compose a total of about ½ of the column length (Figure 16). In *Habenaria*, the stigmaphores support the individual stigmatic lobes, but we have not included this in our diagrams because we are not including characters that are used below the rank of subtribe.

Characters of the Stamen

The stamen is the least modified structure on the column (Table 2, t.s. 14–27). Each flower in the monocotyledons has six stamen positions, only three of which ever bear any structures in the Orchidaceae. Figure 37 illustrates that only the outer median and inner lateral positions are occupied in the orchids. The Neuwiedioideae have all three stamen positions occupied. In the diandrous orchids the inner lateral stamens are retained and the outer median one has developed into a staminode. The monandrous orchids, on the other hand, have retained only the outer median stamen and both of the inner lateral

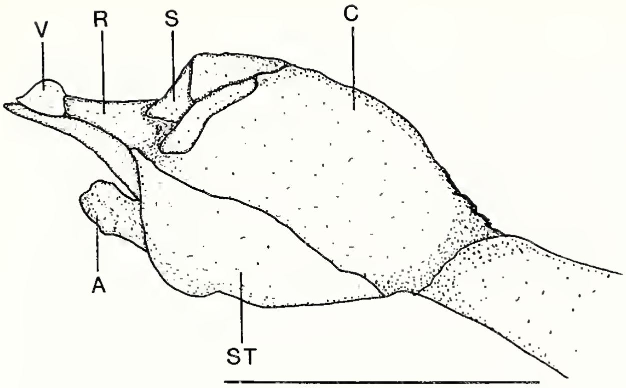


FIGURE 9.—Spiranthoideae, Cranichideae, *Cranichis* sp. Greenwood 825 (AMO).

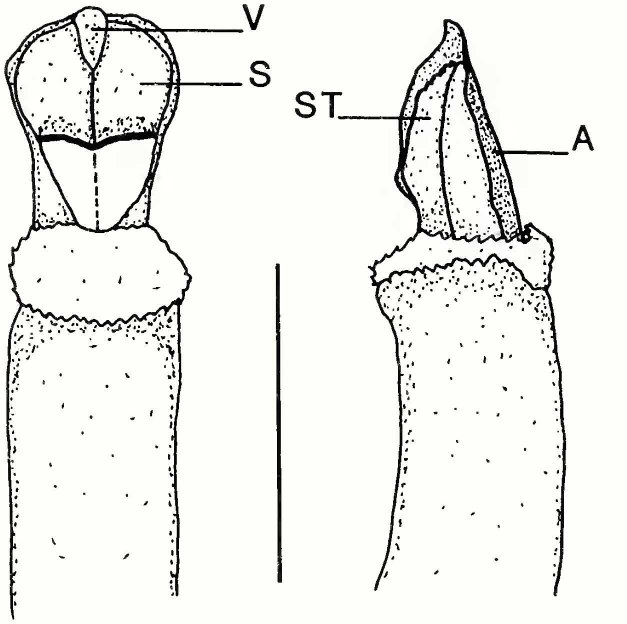
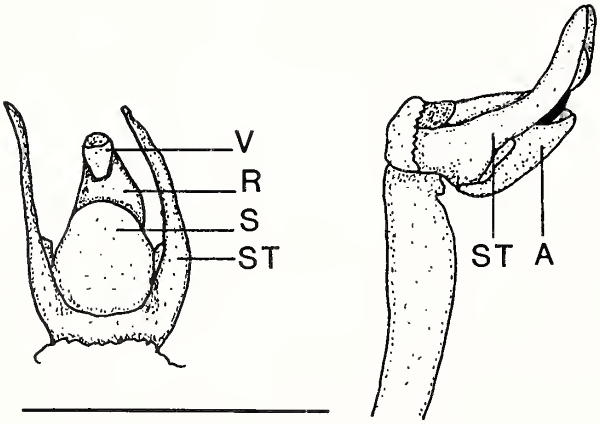


FIGURE 10.—Spiranthoideae, Diurideae, *Diuris maculata* Smith. Clements s.n. (Balogh).



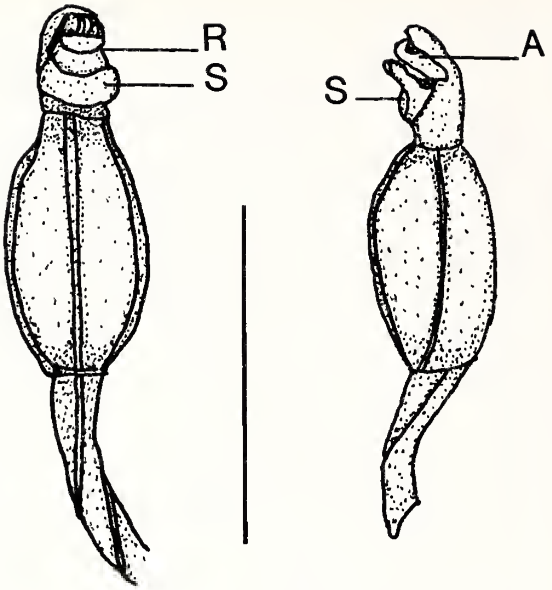


FIGURE 12.—Neottioideae, Neottieae, *Listera ovata* (L.) R. Brown. Kurzweil s.n. (Balogh).

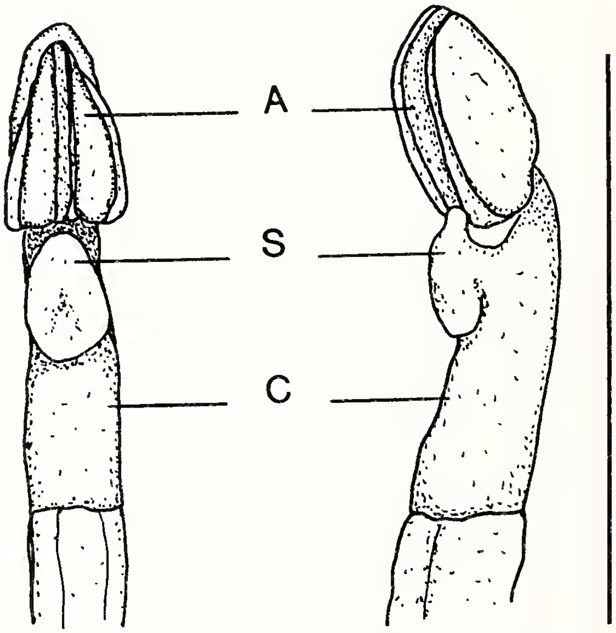


FIGURE 13 (above).—Neottioideae, Neottieae, *Cephalanthera austinae* (A. Gray) Heller. Sandberg and Leiberg 571 (US).

FIGURE 11 (left).—Spiranthoideae, Prasophylleae, *Prasophyllum elatum* R. Brown. Clements s.n. (NCBG).

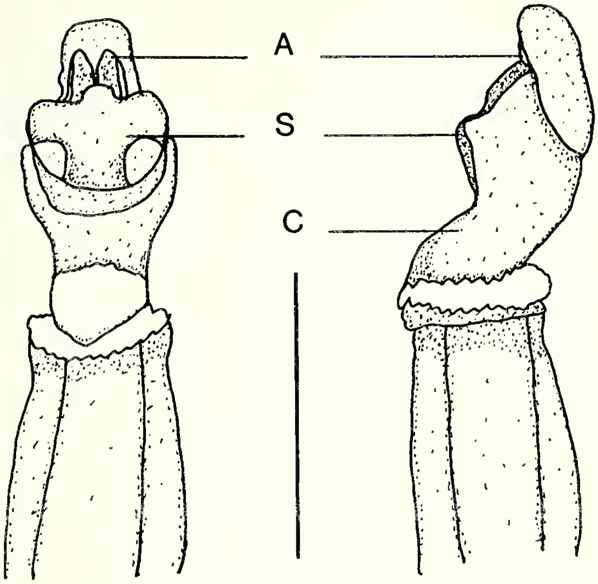


FIGURE 14.—Neottioideae, Neottieae, *Epipactis palustris* (L.) Crantz. Kurzweil s.n. (Balogh).

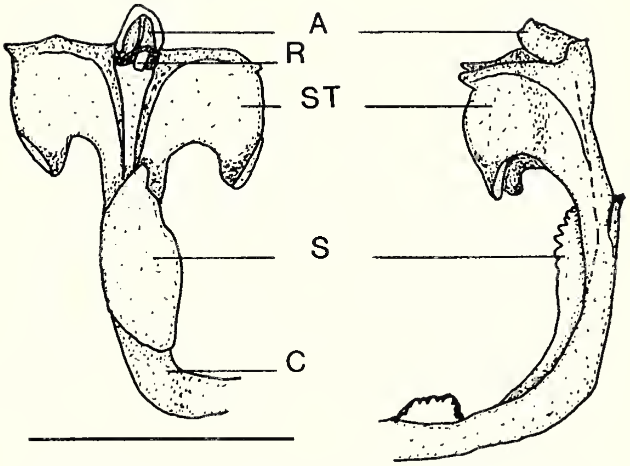


FIGURE 16.—Neottioideae, Pterostylideae, *Pterostylis rufa* R. Brown. Clements s.n. (NCBG).

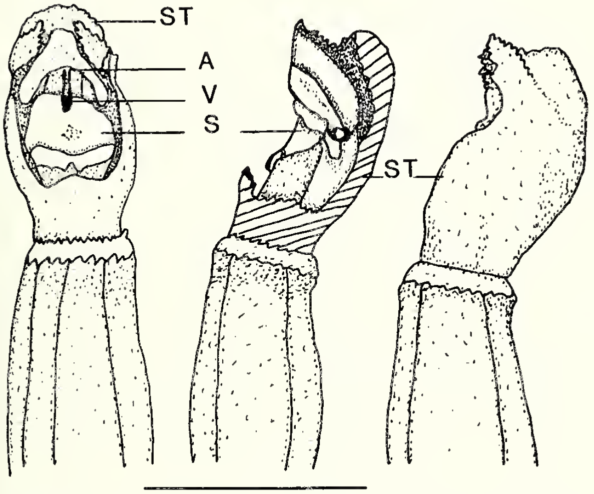


FIGURE 15.—Neottioideae, Thelymitreae, *Thelymitra carnea* R. Brown. Clements 2383 (NCBG).

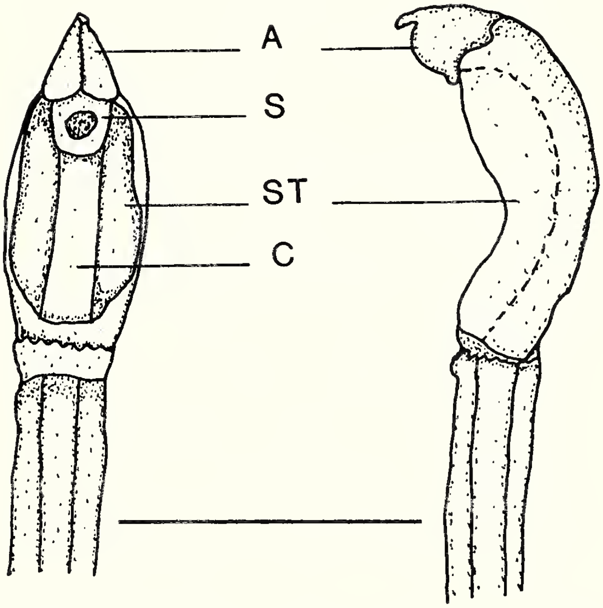


FIGURE 17.—Neottioideae, Geoblasteae, *Caladenia catenata* (Smith) Druce. Clements s.n. (NCBG).

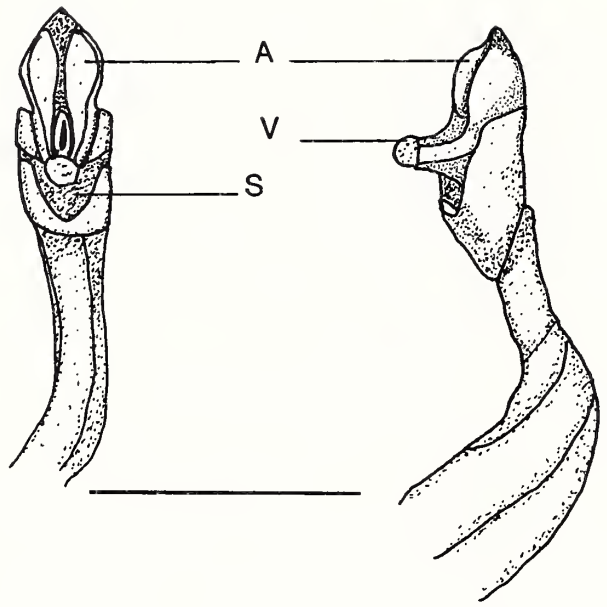


FIGURE 18.—Orchidoideae, Orchideae, *Orchis coriophora* L. Kurzweil s.n. (Balogh).

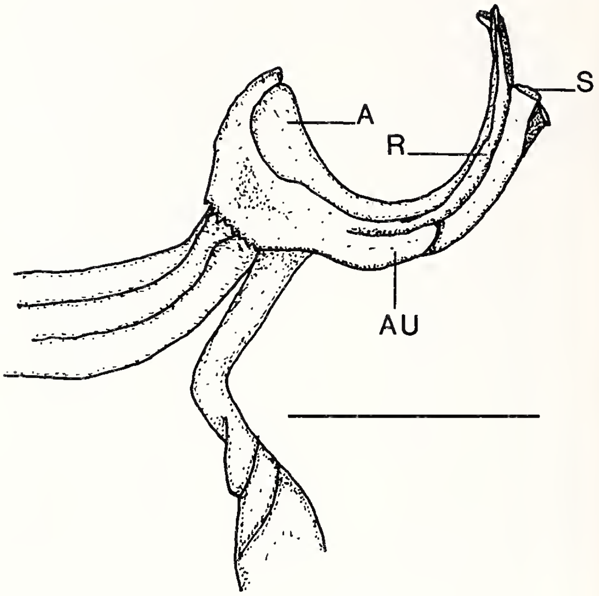


FIGURE 20.—Orchidoideae, Orchideae, *Habenaria genuflexa* Rendle. Kurzweil s.n. (Balogh).

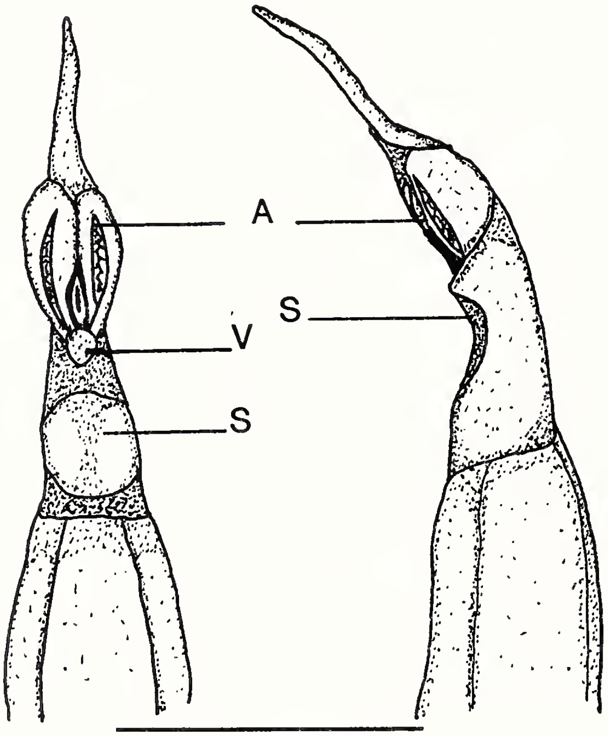


FIGURE 19.—Orchidoideae, Orchideae, *Serapias parviflora* Parl. Kurzweil s.n. (Balogh).

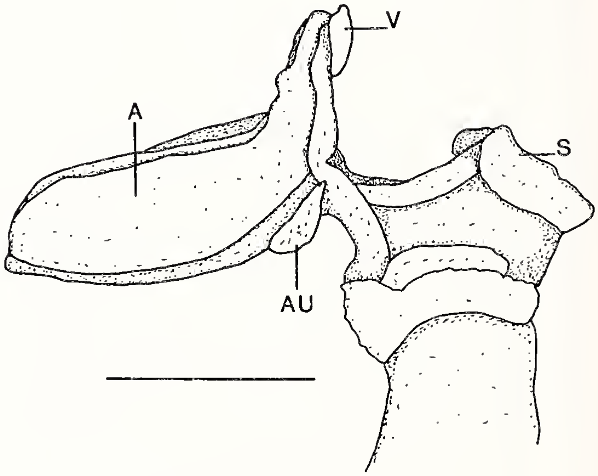


FIGURE 21.—Orchidoideae, Diseae, *Disa crassicornis* Lindley. Wood 8430 (US).

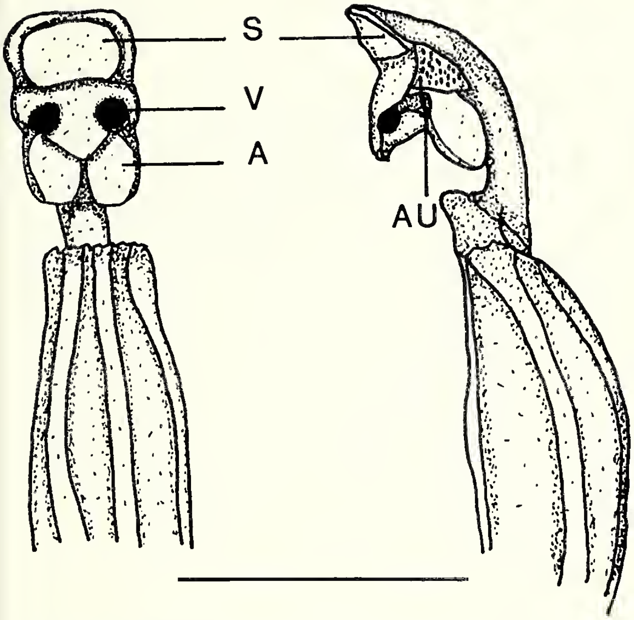


FIGURE 22.—Orchidoideae, Satyrieae, *Satyrium nepalense* Don. Kurzweil s.n. (Balogh).

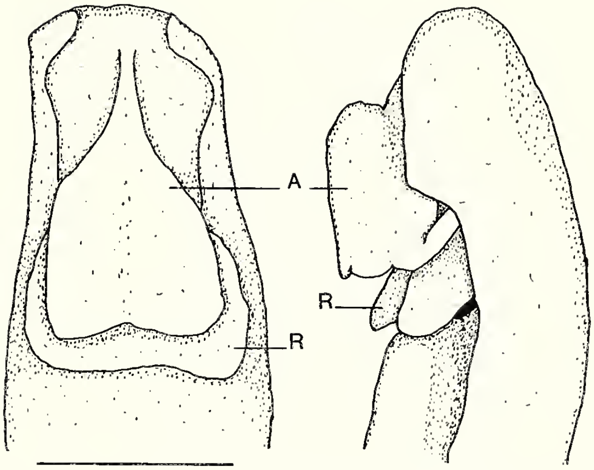


FIGURE 24.—Epidendroideae, Vanilleae, *Vanilla planifolia* Andrews. No collector, s.n. (SEL).

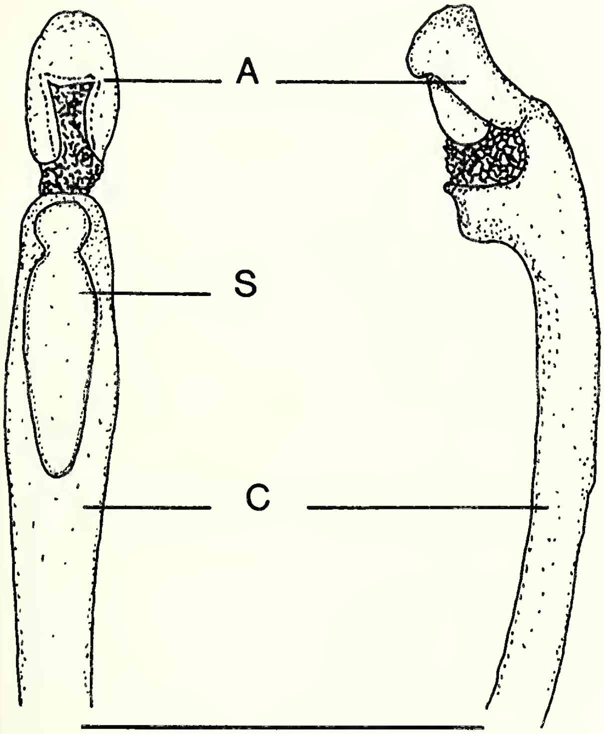


FIGURE 23.—Epidendroideae, Triphoreae, *Triphora trianthrophora* (SW) Rydberg. Greenwood 1150 (AMO).

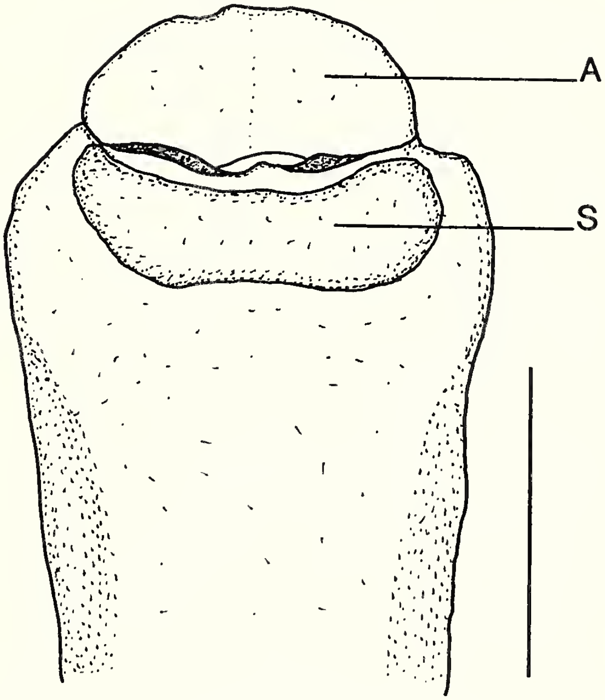


FIGURE 25.—Epidendroideae, Epidendreae, *Arpophyllum* sp. Hagsater 4502 (AMO).

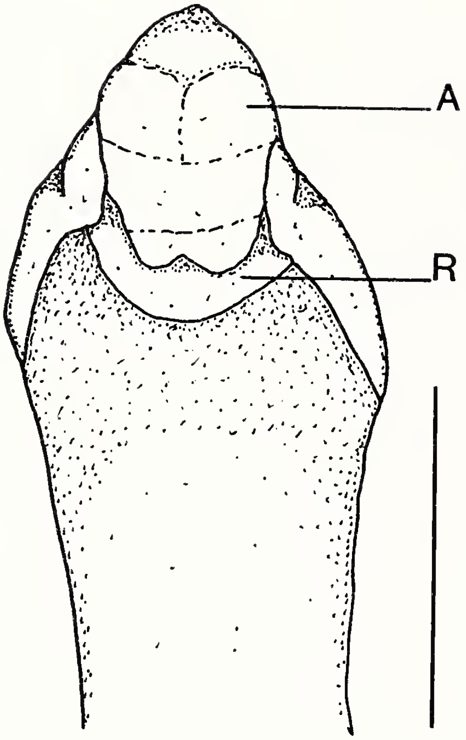


FIGURE 26.—Epidendroideae, Epidendreae, *Bletia* sp. Greenwood 1010 (AMO).

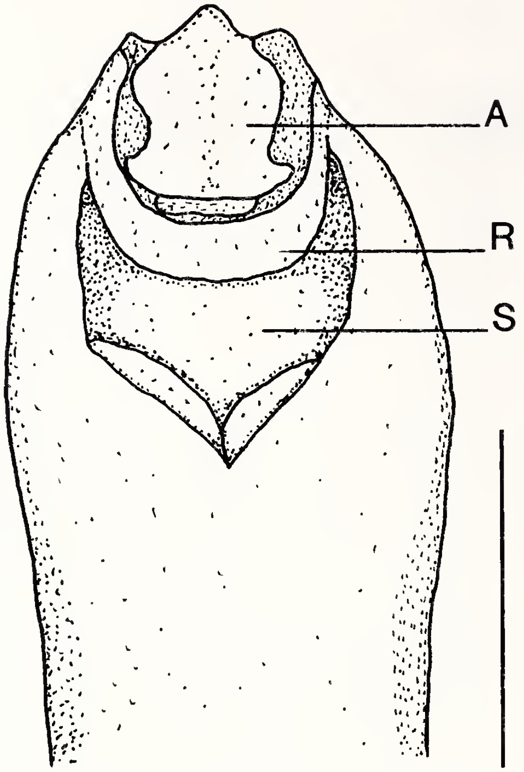


FIGURE 28.—Epidendroideae, Epidendreae, *Coelia bella* Reichenbach filius. Greenwood 540 (AMO).

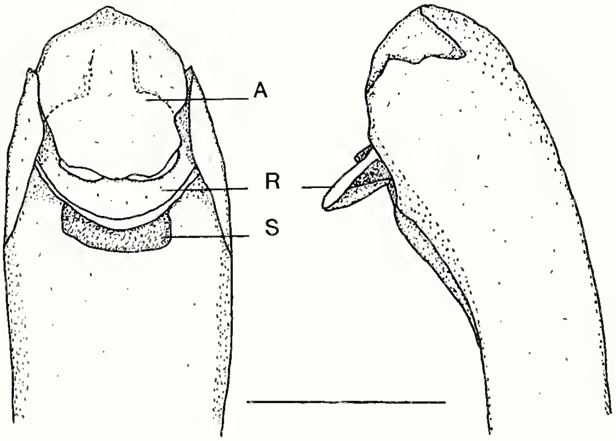


FIGURE 27.—Epidendroideae, Epidendreae, *Hexalectris brevicaulis* L.O. Williams. Greenwood 1059 (AMO).

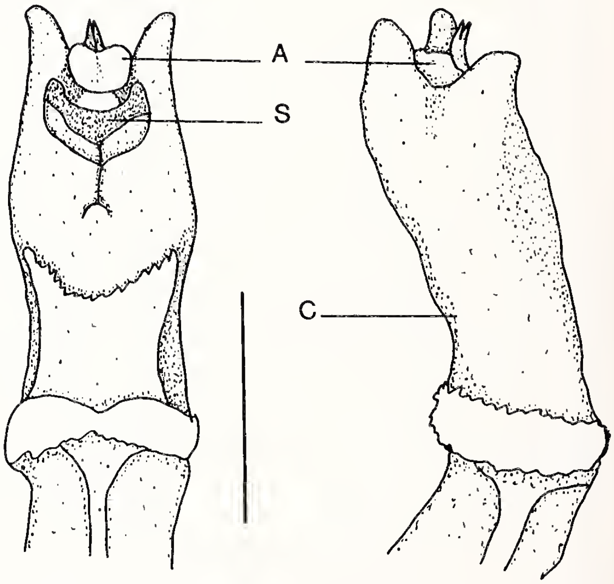


FIGURE 29.—Epidendroideae, Epidendreae, *Encyclia cochleata* (L.) Dressler. Balogh s.n. (Balogh).

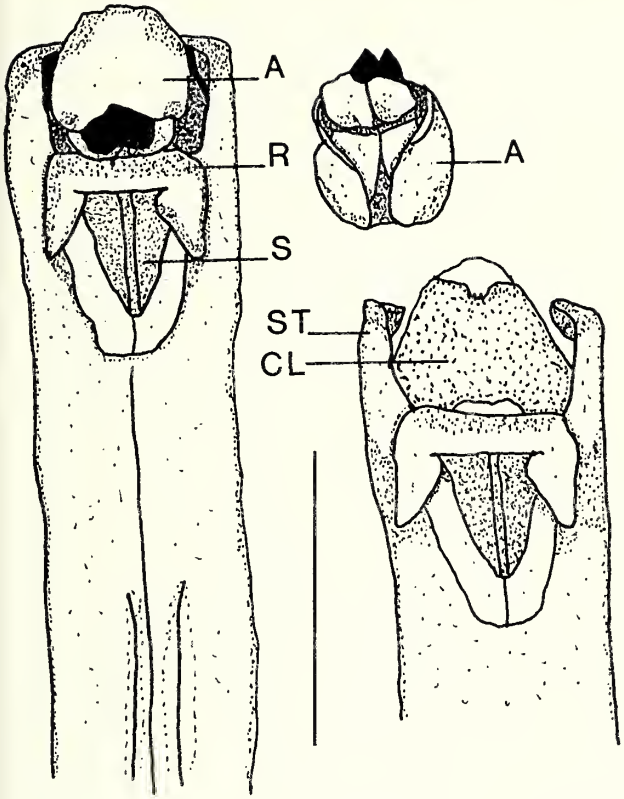


FIGURE 30.—Epidendroideae, Epidendreae, *Sobralia macrantha* Lindley. No collector, s.n. (SI).

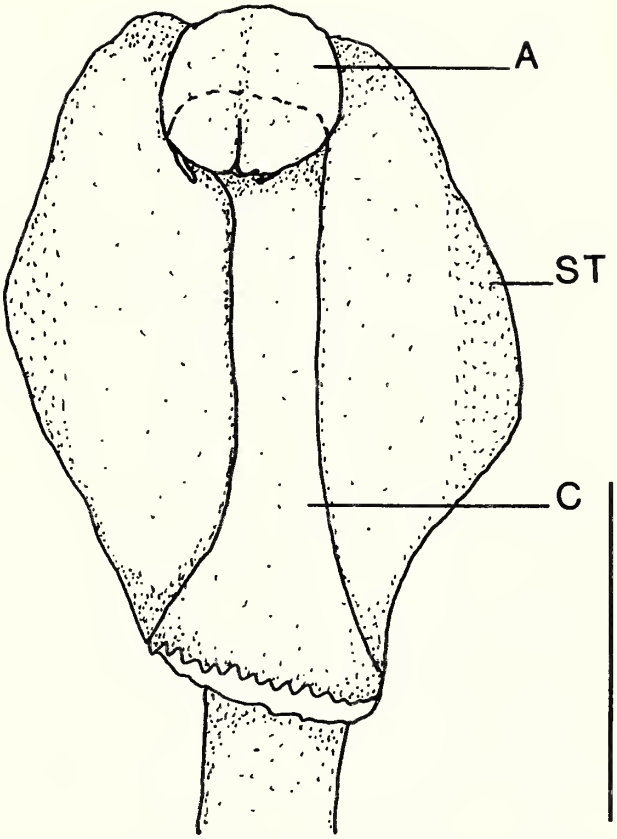


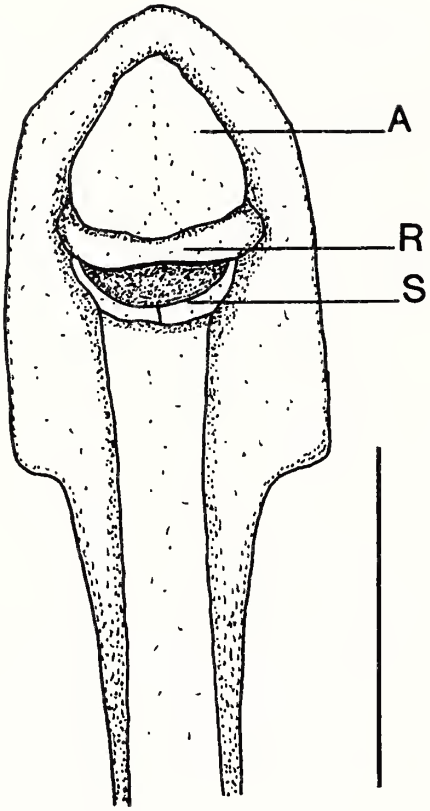
FIGURE 31.—Epidendroideae, Epidendreae, *Calypso bulbosa* (L.) Oakes. Peterson s.n. (Balogh).

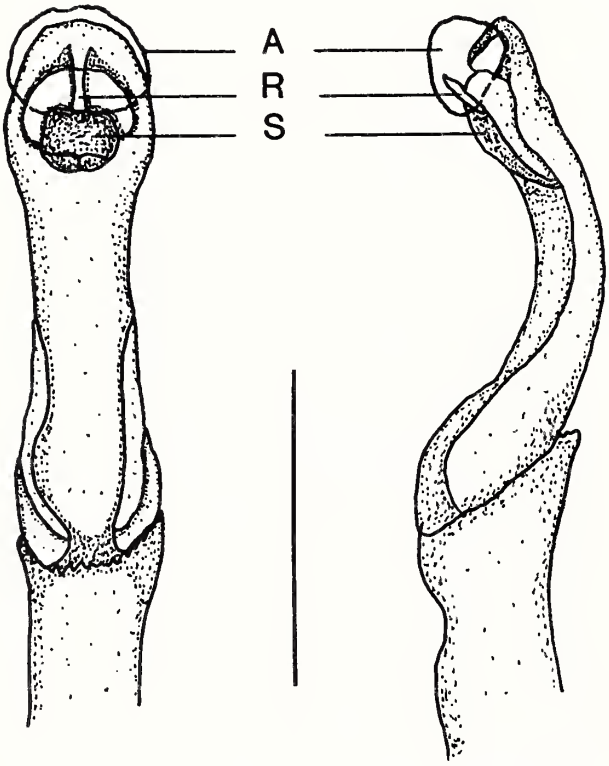
stamens have become staminodes. The only exception to this is in *Diplandorchis*, which has two median stamens, and another Chinese genus, *Tangtsinia*, which has five staminodes and a single outer median stamen. The possession of all three functional stamens is the plesiomorphic condition for transformation series 14 (Table 2). Because the diandrous and monandrous conditions involve different stamens, they are treated as separate apomorphies and are in no way interdependent. Because no relationship is indicated among the staminodes that have developed from different stamens, the characters of the stamens have been divided into those that deal with the outer median stamen (Table 2, t.s. 14–22, Figure 37) and those that deal with the inner lateral stamens (Table 2, t.s. 23–27).

There are other monocot families that exhibit reductions in the number of stamens (Figure 37). In the Zingiberaceae, there is a single functional anther in the inner median position and four staminodes, two in the inner lateral positions and two in the outer lateral positions. The fusion of the two outer staminodes has produced a "labellum" that has replaced the median petal. The Marantaceae also have a single functional anther with the outer stamens represented as staminodes. In the Commelinaceae there are three fertile adaxial stamens in many taxa. Only two families however, have the same type of stamen situation as that found in the orchids. In the Pontederiaceae, *Heteranthera*, has a staminal situation identical to *Neuwiedia*, and *Hydrothrix* has a single median stamen as in the monandrous orchids. In the Philydraceae a single fertile stamen is in the same position as that found in the monandrous orchids (Vermeulen, 1966). Because of the lack of any other similar apomor-

FIGURE 32 (left, upper).—Epidendroideae, Coelogyneae, *Coelogyne mayeriana* Reichenbach filius. No collector, s.n. (SEL).

FIGURE 33 (left, lower).—Epidendroideae, Coelogyneae, *Corallorhiza striata* Lindley. Balogh 977 (US).





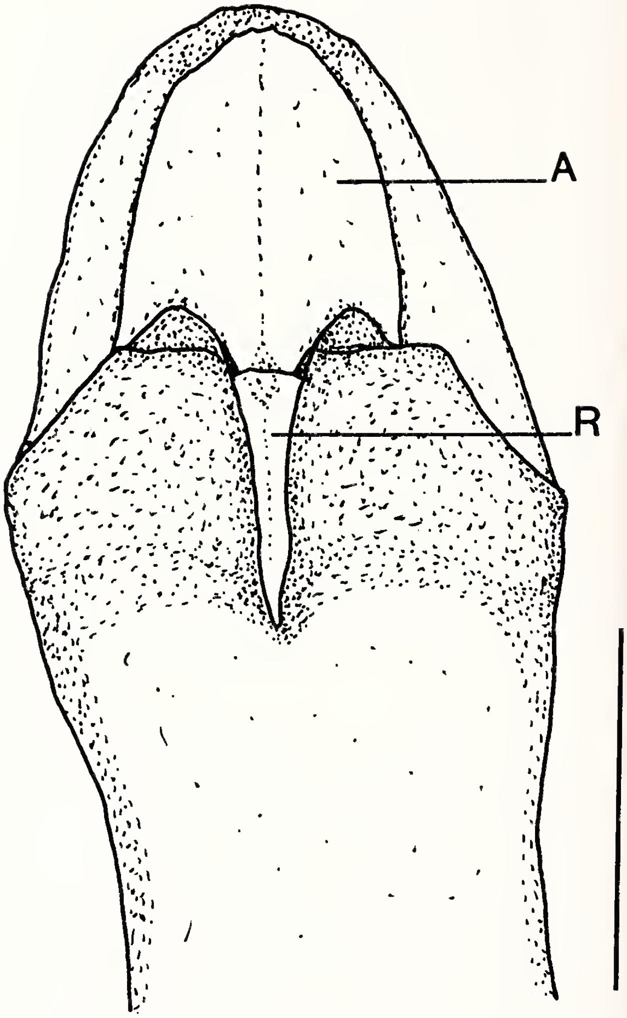


FIGURE 34.—Epidendroideae, Vandeae, *Gongora truncata* Lindley. No collector, s.n. (SEL 105-76-25).

phies, the most parsimonious explanation for these staminal losses is one of parallel evolution, with these characters being autapomorphies for the respective groups. (Autapomorphies are of no use in determining relationships because they found in only one taxon.)

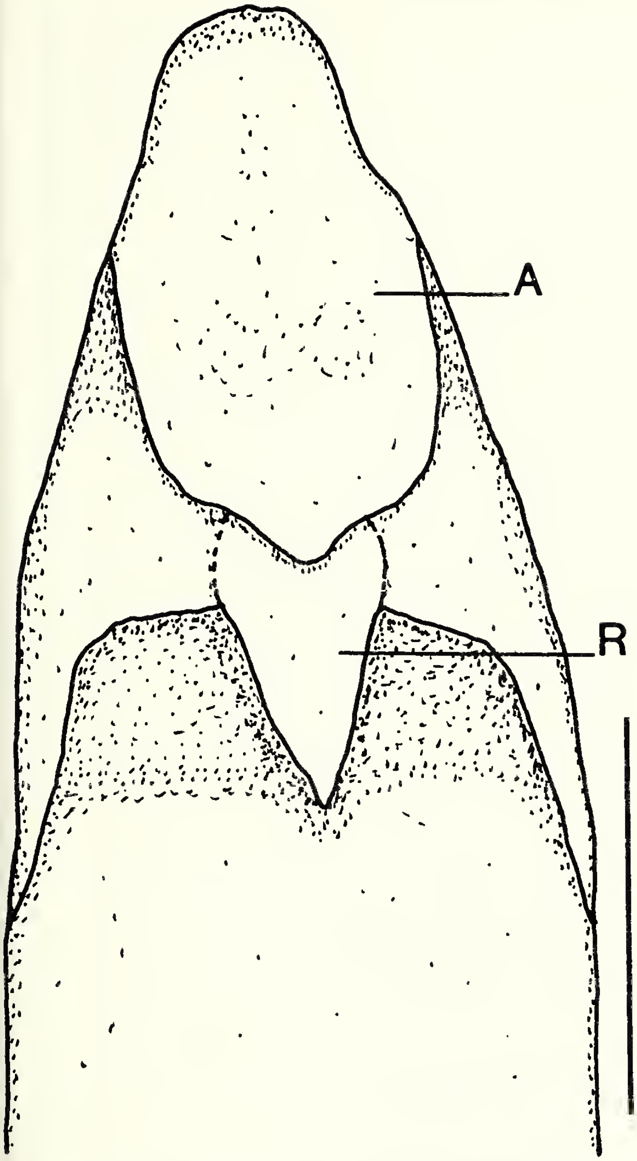


FIGURE 35.—Epidendroideae, Vandeae, *Chondrorhyncha lendyana* Reichenbach filius. No collector, s.n. (SI 79820).

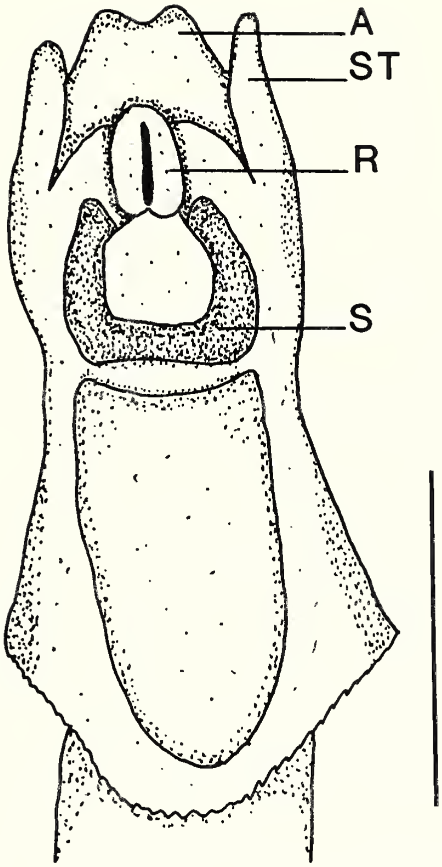


FIGURE 36.—Epidendroideae, Vandeae, *Trichoglottis fasciata* Reichenbach filius. No collector, s.n. (SEL).

Outer Median Anther Position

A unique situation is found in the outer median anther filament of the Thelymitreae. The anther filament is almost completely free of the style but is fused to and incorporated into the staminodal structure (Table 2, t.s. 15; Figure 15). The general condition is the fusion of the filament to the style and the margins of the staminodes.

The outer median anther is inserted on the filament "at or near, rarely below, the base of the stigma" (and parallel to the stigma) (Figures 7–11), "at or near the apex of the stigma" (Figures 12–17), or "above the apex of the stigma" (Figures 18–36), of which the latter two have an anther that extends beyond the stigma apex. Because these two insertions are found only in some groups of orchids and probably nowhere else in the monocots, they are considered to be apomorphic (Tables 2 and 4, t.s. 17). Similarly, the fusion of the anther base to the column apex is found only in the Orchidoideae (Table 2, t.s.

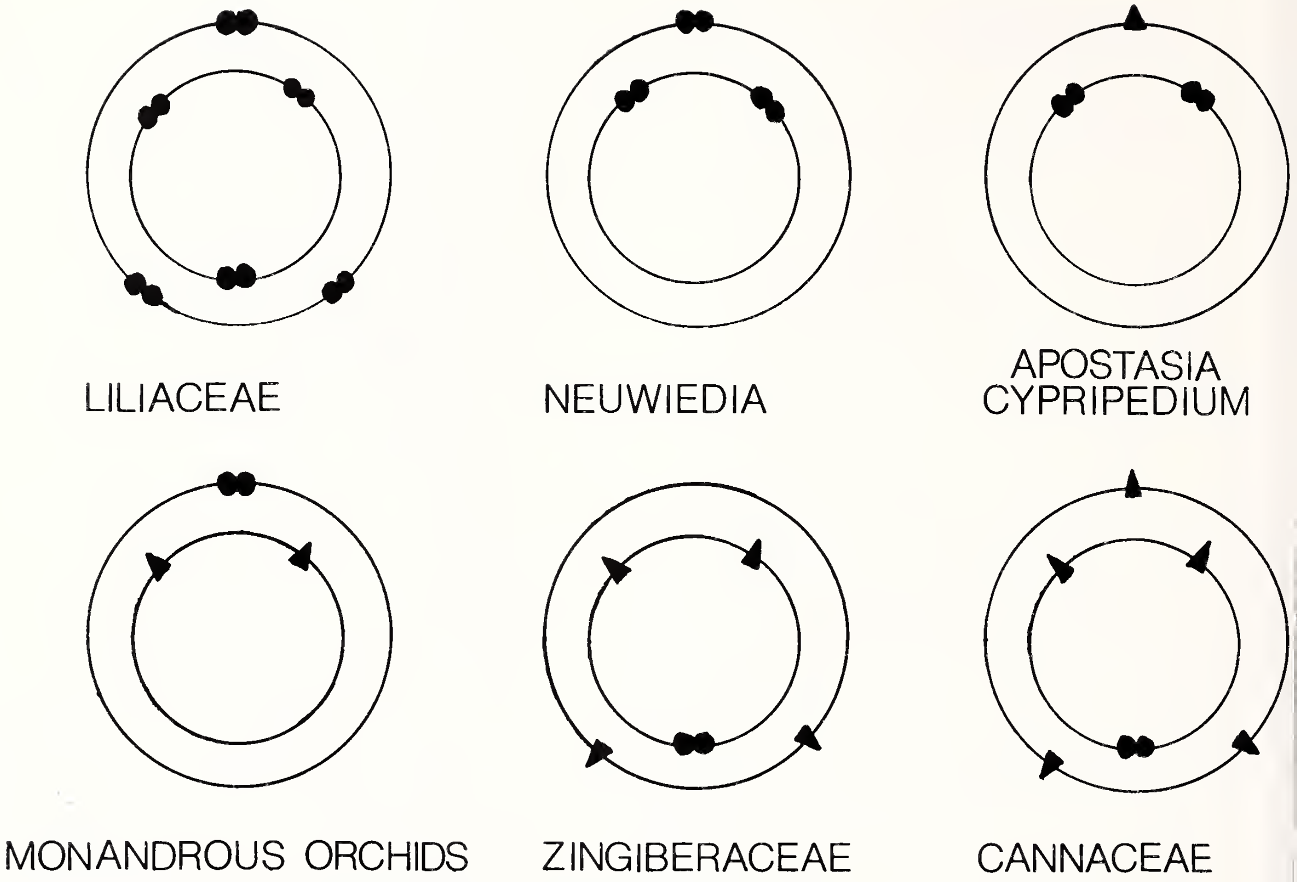


FIGURE 37.—Staminal circles in Liliaceae, Orchidaceae, *Neuwiedia, Apostasia, Cyprepedium,* monandrous orchids), Zingiberaceae, and Cannaceae (triangles = staminodes, double solid circles = anthers). For simplicity all groups are shown in the resupinate condition.

18; Figures 18–22). In the transformation series dealing with the development of the outer median stamen (Table 2, t.s. 19), once again, the plesiomorphic character (erect to suberect) is found in the monocots, e.g., Liliales. The three apomorphic characters—the "upside down" anther (Satyrieae; Figure 22), the anther at right angles to the style (Diseae; Figure 21), and the operculate incumbent to hyperincumbent anther (higher Epidendroideae; Figures 25–36)—are treated as independent of one another.

The majority of orchids have four separate anther locules, like other monocots (although it is often difficult to see the median partitions between the pairs of locules). In some orchids such as the genus *Caladenia* (Geoblasteae), and in some Epidendreae and Pleurothallid groups, the locules are divided so that there may be anywhere from 6 to 12 separate pollen masses (for illustrations see discussion on pollinaria, p. 30). In Pleurothallidinae and isolated Epidendreae, there may be a loss, or perhaps fusion, of two locules so that there appear to be only two pollinia per pollinarium. There are some genera in the Vandeae in which there also appear to be only two pollinia, but this is the result of fusion and there are still four locules. The variation in the number of locule partitions is considered to be apomorphic (Table 2, t.s. 20), however, because the numbers of pollinia are not consistent at the subtribal level in Laeliinae or Pleurothallidinae, they are treated as single apomorphies.

In many of the orchids, especially in tribes Coelogyneae, Maxillarieae, Vandeae, and Epidendreae (sensu Burns-Balogh and Funk) the filament breaks at the juncture of the anther when the pollinarium is removed, causing the anther to fall off the column (Table 2, t.s. 21).

The anther can be either lily-like (plesiomorphic, Figure 3), cap-like (Figures 25–36), or with the connective separating the anther halves at their bases (rarely completely (Figures 18–22; Table 2, t.s. 22). A peculiar situation has been found in two species of *Goodyera*, i.e., *G. repens*, and *G. pubescens*. The anther appears to be similar to that of some Epidendroideae in being nearly incumbent and cap-like on the column apex. There is no doubt that these two closely related species have a specialized anther.

In the diandrous orchids the outer median stamen has developed into a staminode that is either filament-like (Figure 4) or well developed (Figures 5–6). The two situations are treated as independent apomorphies (Table 2, t.s. 16).

Inner Lateral Stamen Positions

There are fewer apomorphic characters concerning the inner lateral stamens/staminodes. Twelve apomorphies are organized into four transformation series (Table 2, t.s. 24–27) and one transformation series is concerned with the adherence of the inner lateral stamen margin (Table 2, t.s. 23). In the Apostasioideae the margins of the stamens and, if present, the margins of the staminode, are adherent marginally into a tube-like structure that surrounds the style for a portion of its length (Figure 4). There is variation in the length of the style in the species of *Apostasia* (de Vogel, 1969). It may be that the style length varies according to age of the plant and that the anthers release their pollen onto the style surface as it grows up through the anther tube (H. Robinson, pers. comm., 1983). This character (Table 2, t.s. 23) is not present elsewhere in the monocots or the orchids. Consequently, it is considered to be apomorphic.

The development of the staminodes and how they are fused with the style is variable (Table 2, t.s. 24). Unfortunately, the distribution of staminodal characters in the Epidendroideae is not well known so that we could not plot the exact distribution for the various types in this subfamily. Each of the known apomorphies are treated as independent of one another (Table 4). There is some question as to whether the auricles found in the Orchidoideae (Table 2, t.s. 25; Figures 18–22) are staminodes or a different structure. Vermeulen (1966) thinks that because there are no vascular traces in the auricles and because when supernumerary stamens develop these structures are also present, that the auricles are not staminodes. Others, such as Schlechter (1970–1984) think auricles are staminodes because they occur in the same position as other staminodes. Whether they are staminodes or not, these structures are easily designated as apomorphies because they have only scattered occurrence elsewhere in the monocots. Dressler (pers. comm., 1983) reports that Vermeulen thinks they also exist in *Allium* while he (Dressler) believes *Lyperanthus* (Orchidaceae) has auricle-like staminodes. If they are treated as staminodes there would be another independent apomorphy in t.s. 24 (Table 2) and t.s. 25 (Table 2) would be deleted.

The clinandrium (Table 2, t.s. 26) is present in two subfamilies, Spiranthoideae and Epidendroideae. In the Spiranthoideae the clinandrium is composed of the back of the stigma/rostellum and the margins of the staminode apices. In the Epidendroideae the clinandrium is composed of the back of the rostellum and probably the margins of the staminode apices.

The final stamen transformation series is concerned with staminode to staminode fusion (Table 2, t.s. 27). In almost all orchids the staminode margins are fused to the column, but in the Thelymitreae the staminode apices are free of any pistil structure and instead are fused to one another (and the filament) to form a hood-like structure over the stigma. In addition the staminodal hood has various ornamentations on it, resembling, for instance, what appear to be stamens or other pollinator attracting devices.

CHARACTERS OF THE POLLINARIUM

Pollinarium structure has been used to circumscribe large groups of orchids (Lindley, 1830–1840; Richard, 1817) and continues to be the source of important characters in the family. The tradition has been maintained to some extent in this classification as most major groups are defined by at least one apomorphy of the pollinarium.

In the monandrous orchids the pollen masses and any accessory structures take on a characteristic shape called the pollinarium. The shape of this structure is usually diagnostic to genus (rarely to species). Naturally, a powdery, unstructured pollen mass or pollinium is the plesiomorphic condition. There are three apomorphic types of pollen aggregation (Table 2, t.s. 35): granulate, composed of monads or tetrads (Figures 38–42, 48–50, 52, 57–62); sectile or massulate, composed of packets of tetrads, rarely monads (Figures 43–47, 51, 53–56, 63–65); and pollinia, hard and waxy, composed of compacted tetrads that share a common wall (Figures 66–84). Each of these was treated as an apomorphy independent of the other. A very rare condition occurs in *Chiloglottis* (Geoblasteae), which has sectile pollinia composed of monads (Figures 51, 53) or tetrads (Ackerman and Williams, 1981).

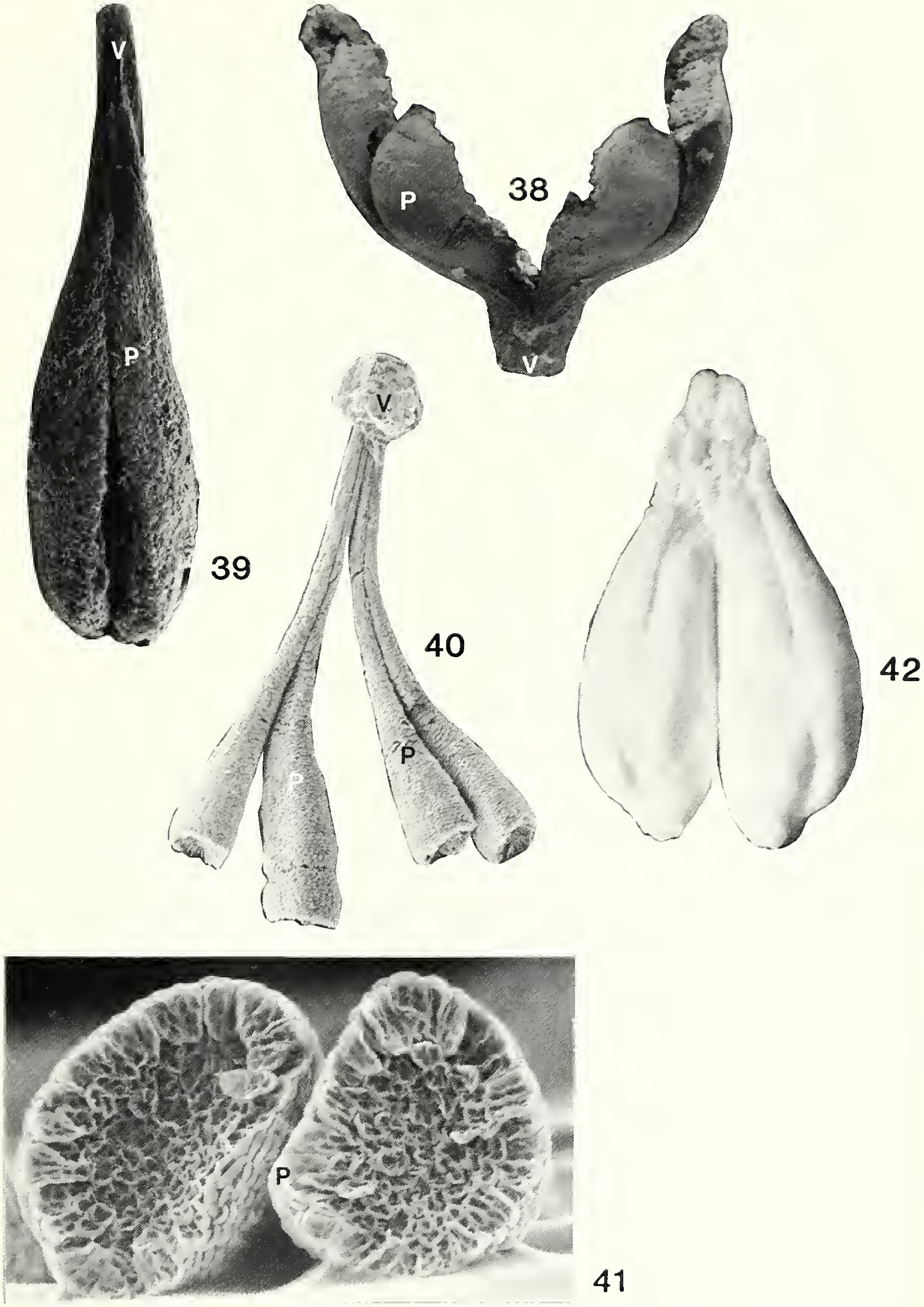
The majority of orchids have some type of accessory structure accompanying the pollinia and viscidium (Table 2, t.s. 28–30). These structures can be pollen-embedded caudicles or sterile caudicles with a stipe (Table 2, t.s. 28). Some members of the Spiranthoideae and the Neottioideae have the simplest type of pollinarium, i.e., four pollinia and a viscidium (Figures 38–42). In the Orchidoideae a tail-like sterile caudicle (Table 2, t.s. 29) and viscidium accompany the sectile pollinia (Figures 54–56). All of the above types are found in Epidendroideae in addition to fused pollen-embedded caudicles (Table 2, t.s. 30; Figures 78–79) and extremely reduced pollen-embedded caudicles (Figure 71). The Dendrobieae and Malaxideae (Figures 72–73) lack any specialized structures (except for one species of *Bulbophyllum* that has a hamular stipe). All apomorphies were treated as independent of one another (Table 2).

In most orchids the pollinia have a definite polarity with the apex attenuate and the base rounded, as in the Spiranthoideae (Figures 38–47) and some Epidendroideae (Figures 68–70). In the Orchidoideae and Neottioideae the pollinia have a rounded apex and attenuate, sometimes rounded base, the result of the basitonic attachment of the viscidium (Figures 48, 49, 51, 52, 54, 55). In most Epidendroideae the pollinia are rounded at both the apex and base (Figures 56, 71–84). All three conditions are considered apomorphies and are treated independently (Table 2, t.s. 32).

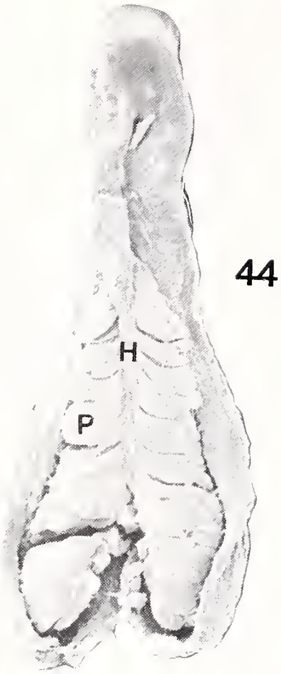
Elastoviscin (Table 2, t.s. 37) is a male sporogenous breakdown product that is probably present in all monandrous orchids in some form (Rasmussen, 1983; pers. comm., 1983; pers. observ. by Burns-Balogh). In the Spiranthoideae (Figure 46) and the Neottioideae (Figure 53) the elastoviscin is elusive in nature. For example, in *Ludisia discolor* elastoviscin may or may not be present (Figure 46) and in *Sarcoglottis* some species may or may not have degenerated pollen tetrads (elastoviscin) at the very apex of the pollinia. It may also take the form of a thin sheath-like layer around the pollinia. In these two subfamilies the presence of elastoviscin is considered to be too variable to use as a character. In some Spiranthoideae, Orchidoideae and Epidendroideae the elastoviscin takes the form of a tail-like or connective caudicle (mentioned above).

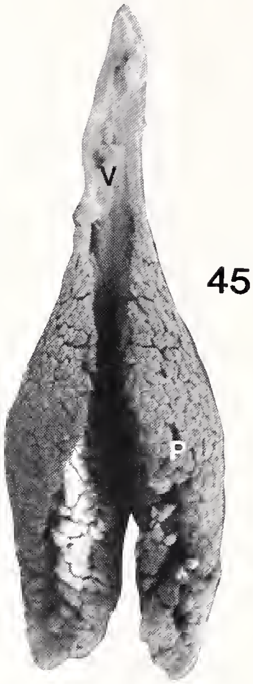
The pollen unit in subfamilies Neuwiedioideae, Apostasioideae, and Cypripedoideae are monocolpate monads (Table 2, t.s. 36 and 39), but in the monandrous orchids the pollen unit is usually a monoporate tetrad. In subfamily Neottioideae and some lower Epidendroideae the pollen unit can be either a monoporate monad or

FIGURES 38–84.—Pollinarium morphology of the Orchidaceae. Key to letter symbols: V = viscidium, H = hamular stipe, P = pollinia, E = elastoviscin, M = massular, S = tetrad sheath, PO = pore, C = caudicle, T = tegular stipe.

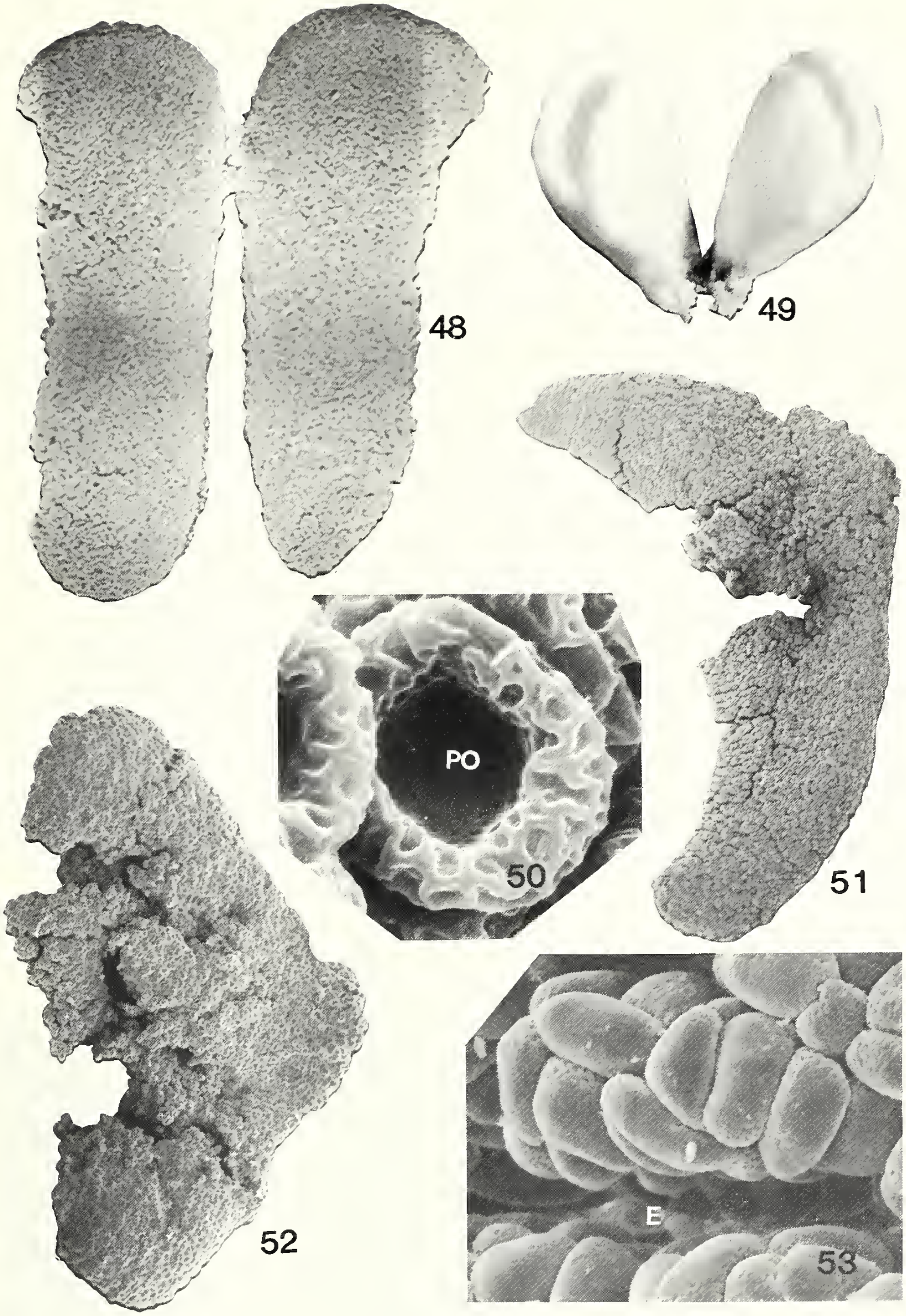


FIGURES 38–42.—Spiranthoideae: 38, Cryptostylidinae, *Cryptostylis subulata* (Labill) H.G. Reichenbach filius. Bernhardt s.n. (Balogh), × 20; 39, Spiranthinae, *Spiranthes lacera* (Raffinesque) Raffinesque. Balogh 904 (US), × 30; 40, 41, Cranichidinae, *Solenocentrum costaricense* Schlechter. Dressler 5841 (Balogh), × 50, × 150; 42, Diurideae, *Diuris maculata* Smith. Bernhardt s.n. (Balogh), × 25.

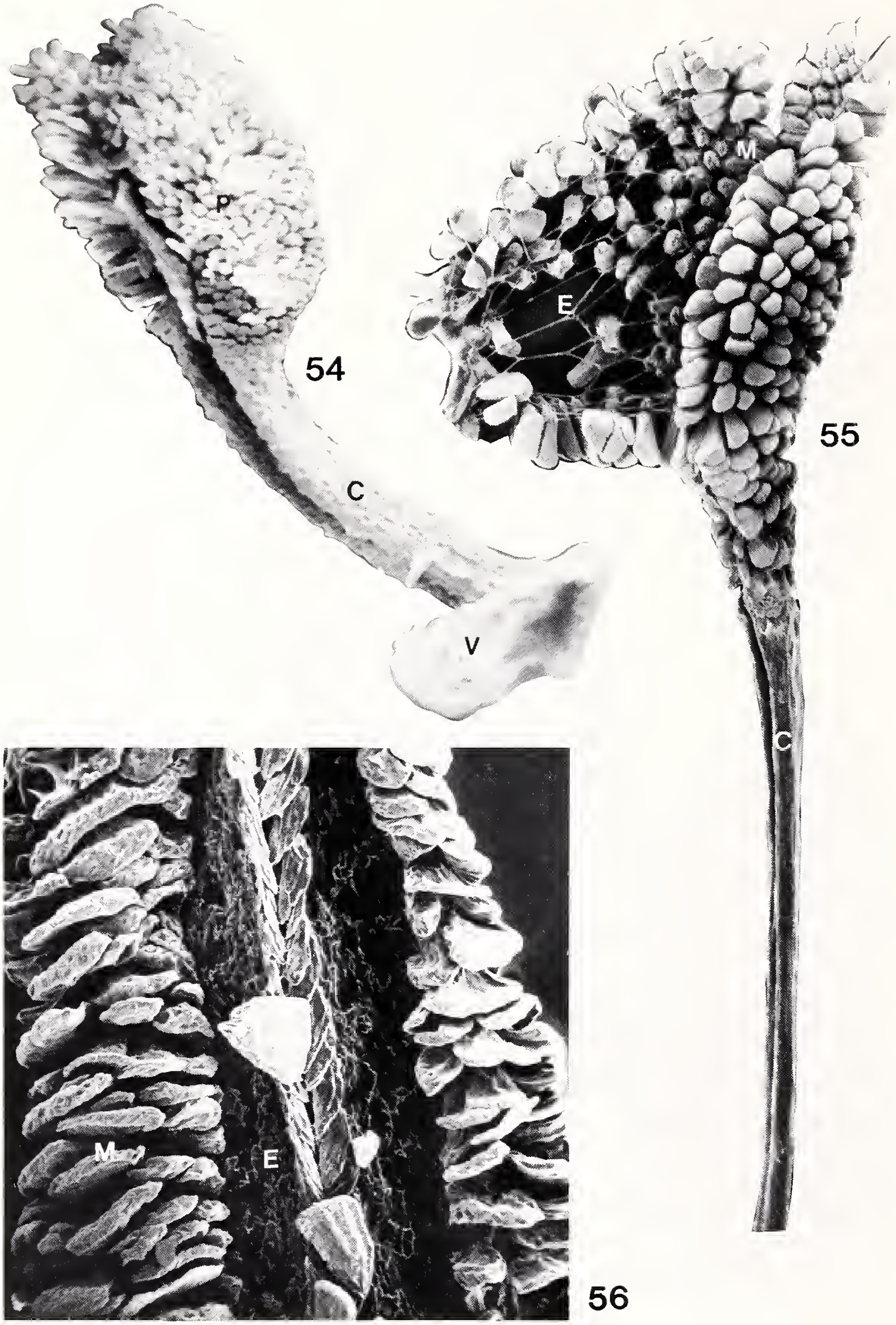




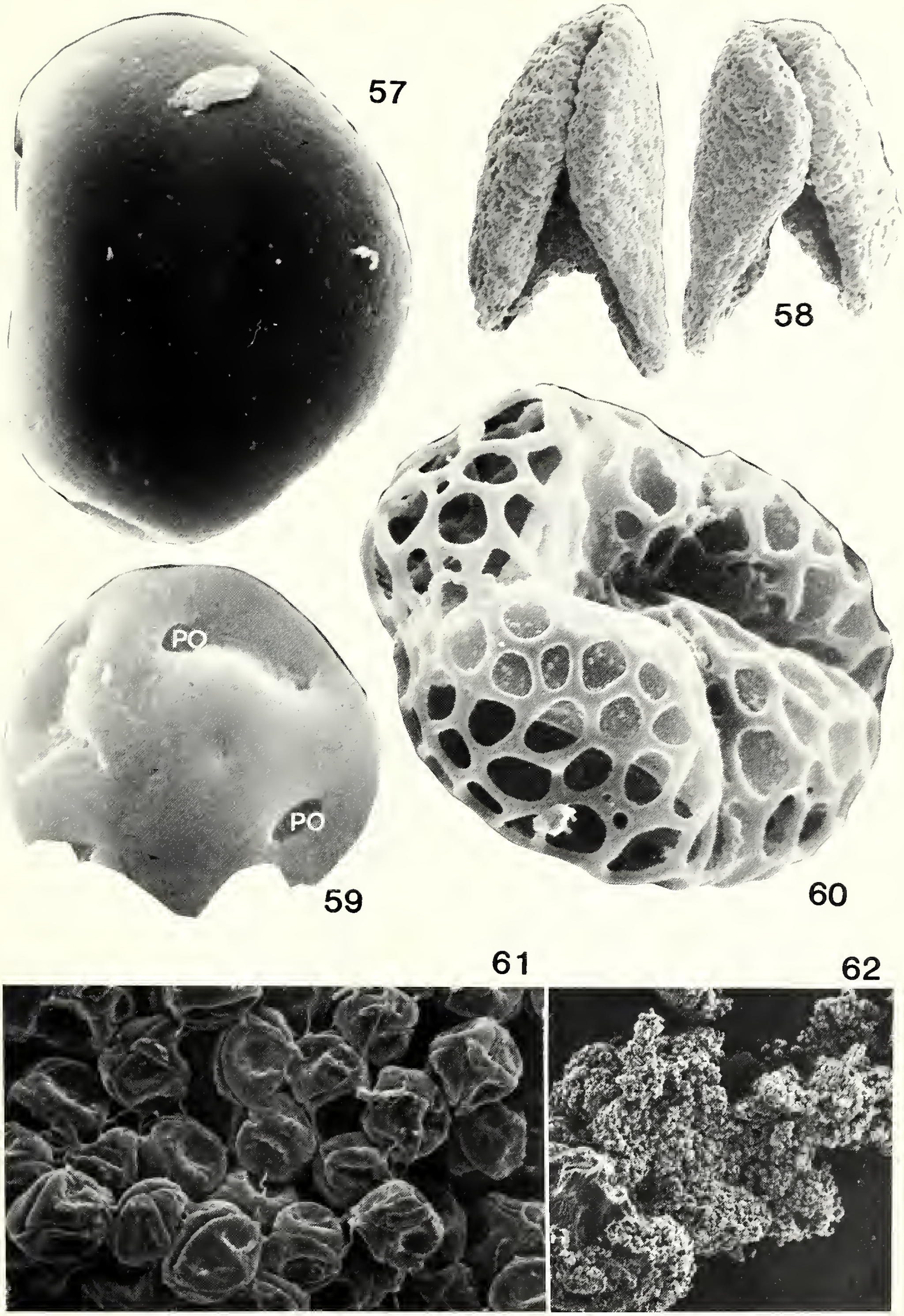
FIGURES 43–47.—Spiranthoideae: 43, Prasophylleae, *Prasophyllum suttonii* R. Rogers and B. Rees. J.T. 1340 (SEL), × 40; 44, Tropidinae, *Corymborkis forcipigera* (Reichenbach filius and Warcs.) Williams. Turckheim 860 (US), × 40; 45–47, Goodyerinae: 45, *Goodyera oblongifolia* Rafinesque. Balogh 1055 (US), × 30; 46, *Ludisia discolor* (Ker-Gawl.) Richards. Balogh s.n. (Balogh), × 50; 47, *Physurus sagreanus* Richards. Jimenez 2757 (US), × 150.



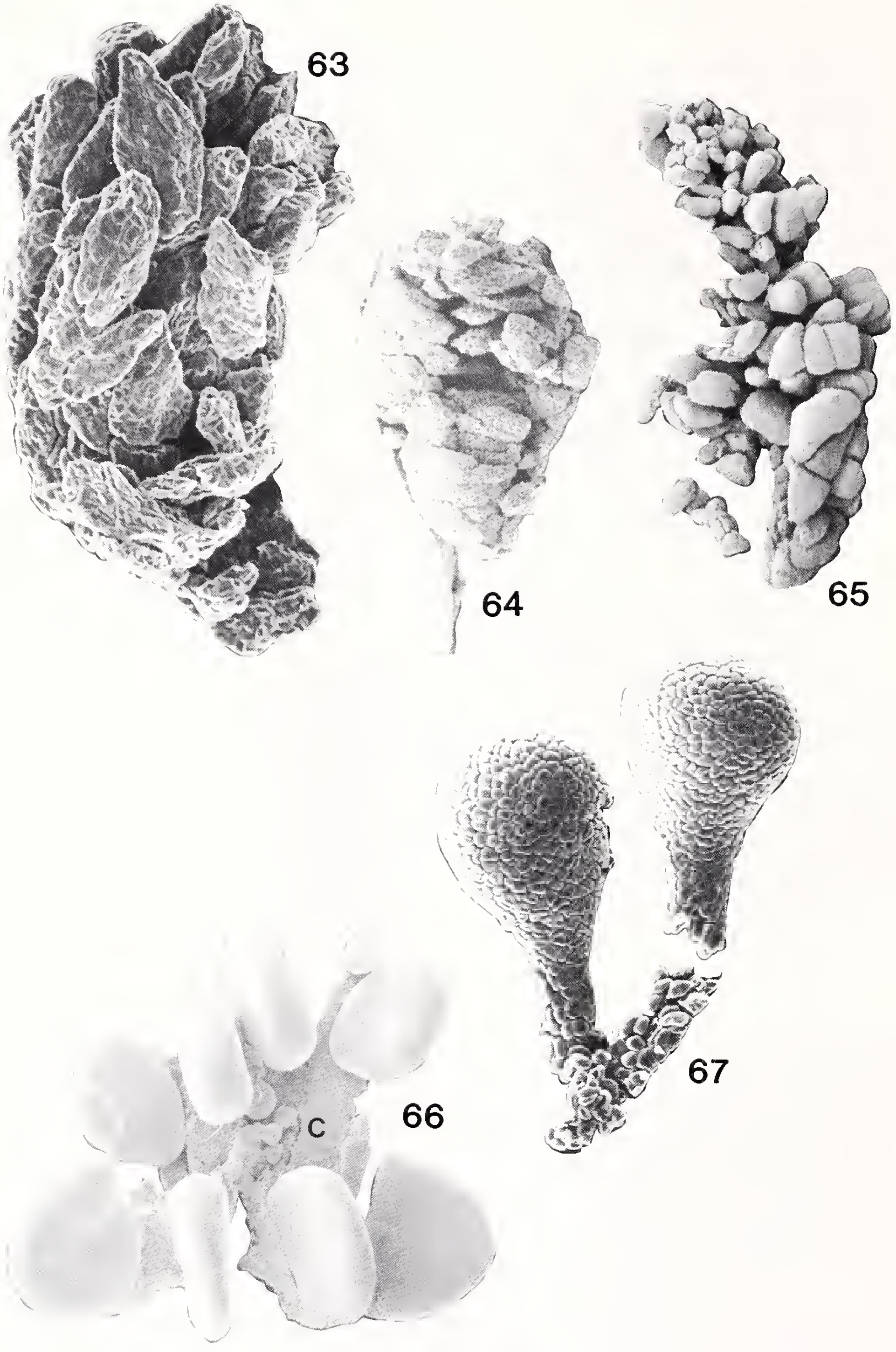
FIGURES 48–53.—Neottioideae: 48, Pterostylideae, *Pterostylis baptisii* Fitzgerald. Bernhardt s.n. (Balogh), × 90; 49, Thelymitreae, *Thelymitra carnea* R. Brown. Clements 2383 (NCBG), × 30; 50, Neottieae, *Epipactis gigantea* Douglas ex Hooker. Hall 2370 (US), × 2000; 51–53, Geoblasteae: 51, 53, *Chiloglottis gunnii* Lindley, Bernhardt s.n. (Balogh), × 50, × 750; 52, *Caladenia (carnea) catenata* (Smith) Druce. Bernhardt s.n. (Balogh), × 60.



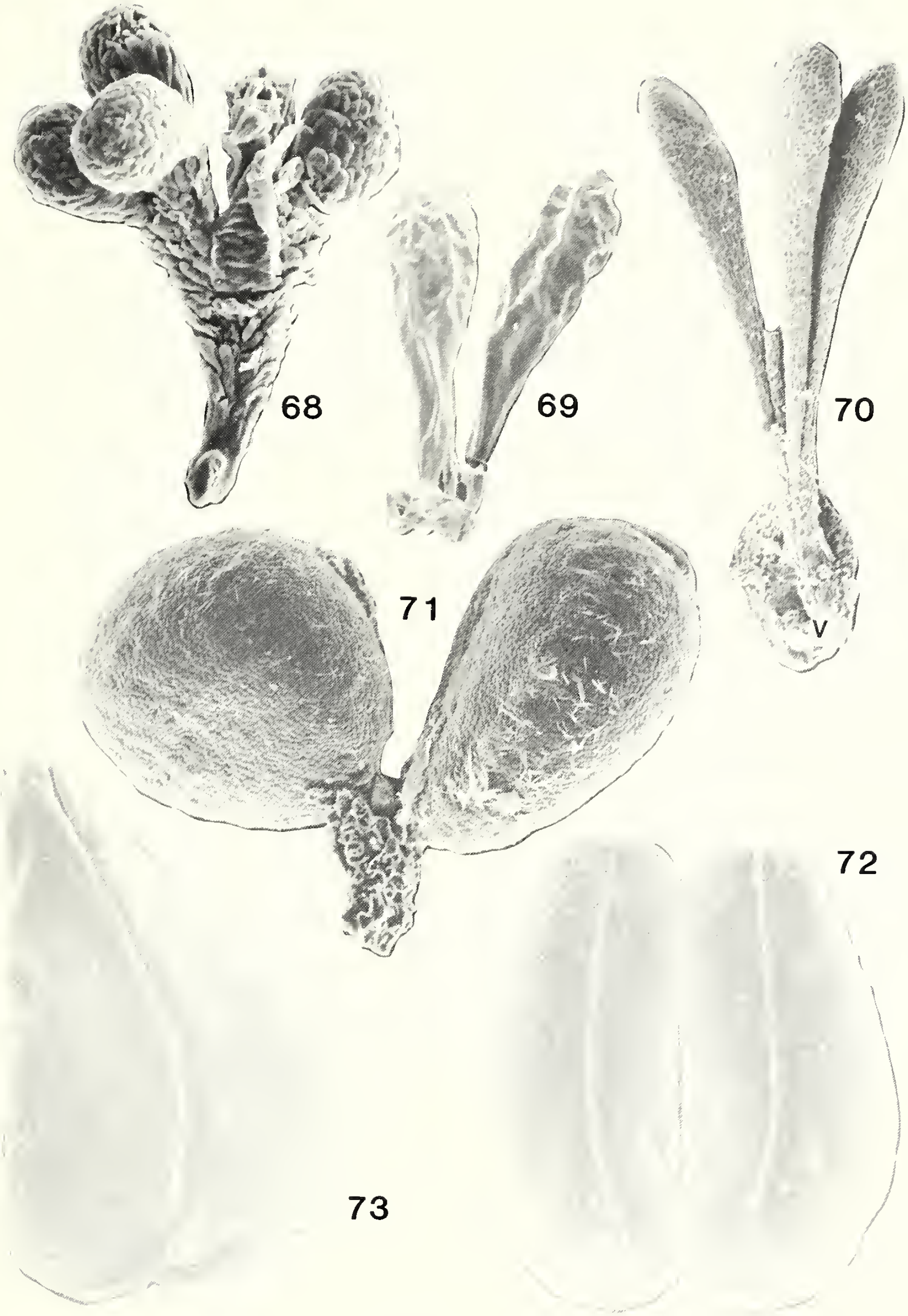
FIGURES 54–56.—Orchidoideae: 54, Satyrieae, *Satyrium corrifolium* SW. Clements s.n. (NCBG), × 40; 55, Diseae, *Disa crassicornis* Lindley, Wood 8430 (US), × 50; 56, Orchideae, *Habenaria* sp., Balogh 727 (US), × 35.



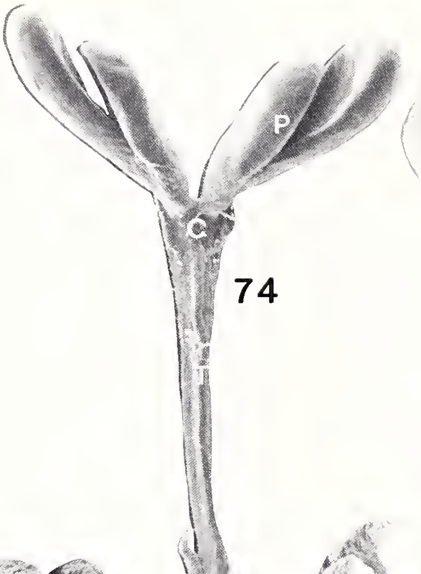
FIGURES 57–62.—Epidendroideae, Vanilleae: 57, *Vanilla pauciflora* Dressler, Dressler s.n. (Balogh), × 3500; 58, *Palmorchis* sp., Dressler s.n. (Balogh), × 100; 59, *Lecanorchis brachycarpa* Ohwi, Ohiui and Walker 7023 (US), × 3000; 60, 62, *Psilochilus* sp., Dressler s.n. (Balogh), × 2500, × 35; 61, *Cleistes divaricata* (L.) Ames, Chapman s.n. (US), × 500.



FIGURES 63–67.—Epidendroideae. 63–65, Gastrodieae: 63, *Gastrodia sesamoides* R. Brown. Bernhardt s.n. (Balogh), × 40; 64, *Epipogium aphyllum* (Schmidt) SW, Baenitz s.n. (US), × 20; 65, *Arethusa bulbosa* L. Cheney, s.n. (US), × 100; 66, 67, Epidendreae: 66, *Arpophyllum giganteum* Hartweg ex Lindley, Suarez 171 (AMO), × 100; 67, *Schomburgkia tibicinis* Bateman, Greenwood s.n. (AMO), × 40.



FIGURES 68–73.—Epidendroideae. 68–70, Pleurothallis group: 68, *Octarrhena condensata* (Ridl.) Holtt., Dressler s.n. (Balogh), × 200; 69, *Lepanthes* sp., Suarez 294 (AMO), × 100; 70, *Meiracyllium trinasutum* Reichenbach filius. Dressler, s.n. (Balogh), × 55; 71–72, Dendrobieae: 71, *Sunipia racemosa* (SM) T. Tang and F.T. Wang, Dressler s.n. (Balogh), × 130; 72, *Dendrobium discolor* Lindley, Bernhardt s.n. (Balogh), × 50; 73, Malaxideae, *Malaxis marsupichila* Upton, Clements 1148 (NCBG), × 200.



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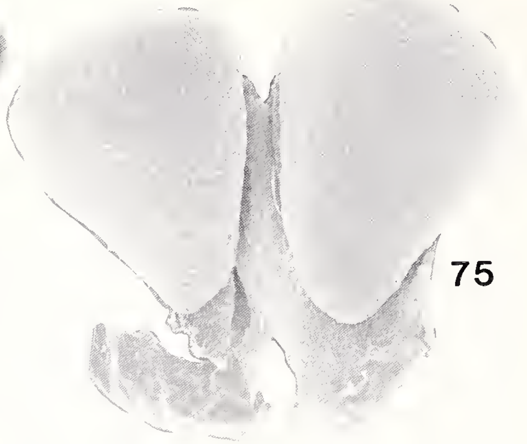

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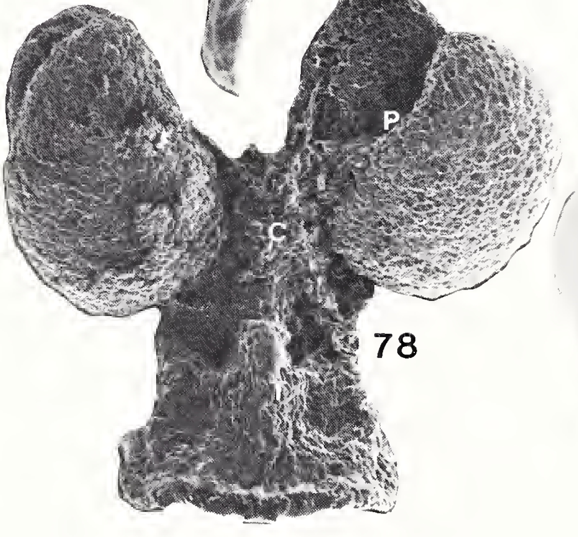

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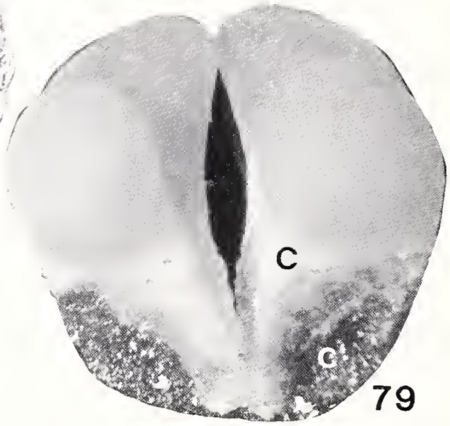

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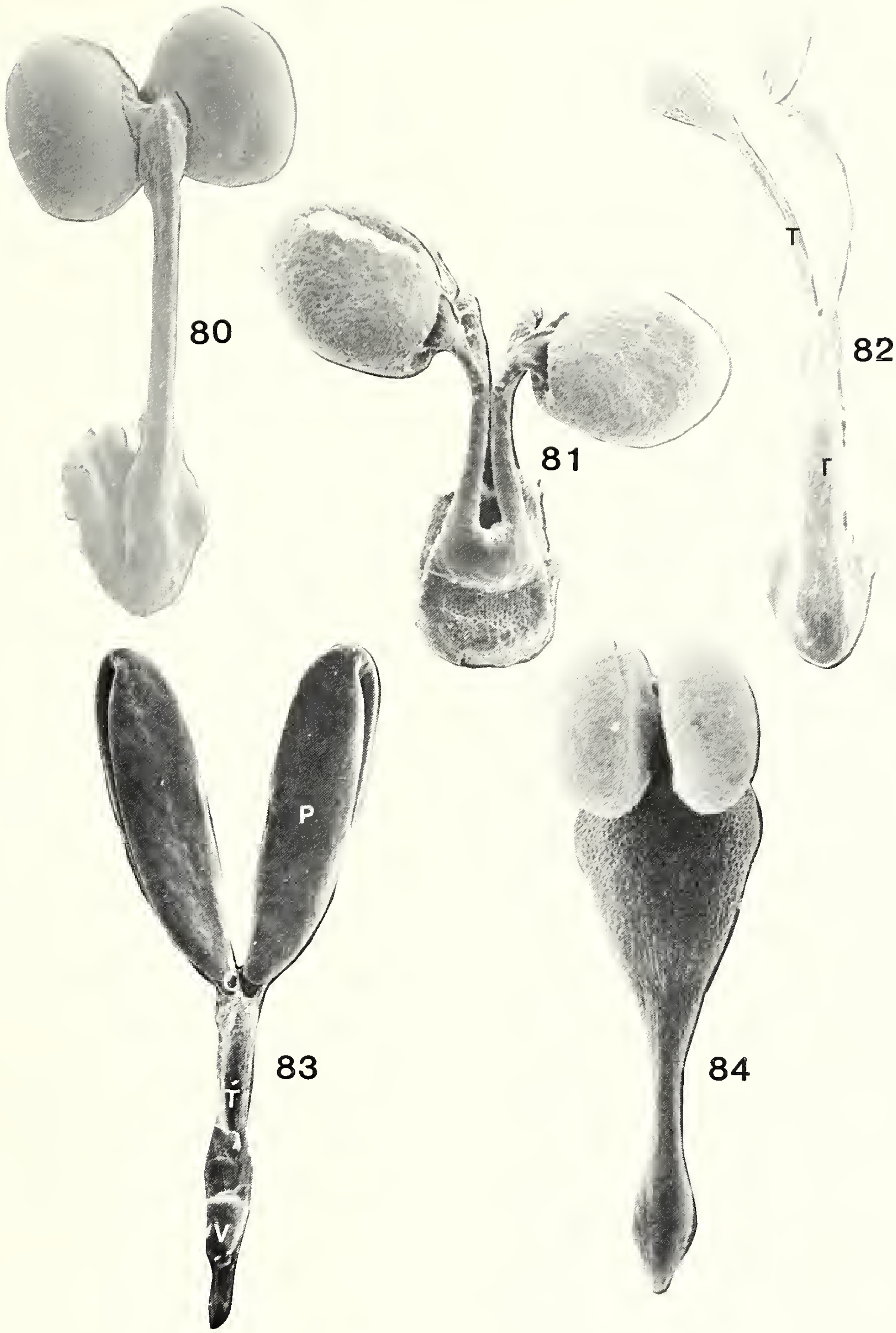
FIGURES 74–79.—Epidendroideae. 74–77, Maxillarieae: 74, *Telipogon klotscheanus* Reichenbach filius, Dressler s.n. (Balogh), × 30; 75, *Calypso bulbosa* (L.) Oakes, Peterson s.n. (Balogh), × 40; 76, *Cryptarrhena guatemalensis* Schlechter, Dressler s.n. (Balogh), × 80; 77, *Maxillaria* sp., Balogh 815 (US), × 30. 78–79, Coelogyneae: 78, *Govenia liliacea* (Llave and Lex) Lindley, Greenwood 556 (AMO), × 55; 79, *Coelogyne pandurata* Lindley, no collector, s.n. (SI), × 25.



FIGURES 80–84.—Epidendroideae, Vandeae: 80, *Gastrochilus bellinus* Kuntz, no collector, s.n. (Frankfurt Botanical Garden), × 20; 81, *Dipodium punctatum* (Smith) R. Brown, Bernhardt s.n. (Balogh), × 40; 82, *Fernandezia hartwegii* (Reichenbach filius) Garay and Dunsterville, Dressler s.n. (Balogh), × 50; 83, *Gongora gratulabunda* Reichenbach filius, Mejia s.n. (Balogh), × 20; 84, *Plectrophora alata* (Rolfe) Garay, JFM 882 (SEL).

tetrad. A specialized condition is found in *Lecanorchis* and *Epistephium* (Figure 59) (Ackerman and Williams, 1980; Burns-Balogh and Robinson, 1985) and possibly *Vanilla* (Figure 57) in which the monad is polyporate. The tetrad condition is considered to be the apomorphic character because almost all other monocots have pollen dispersed as monads.

There are a number of transformation series dealing with the pollinia that have only one apomorphic character and are easily polarized because they are found in restricted groups and no where else in the monocots:

1. In most orchids the pollinia are side by side (Table 2, t.s. 31; e.g., Figures 39–41); in the vandoid orchids, however, there is a situation called superposed pollinia in which the locules have moved to the margins of the anther and the pollinia in each set have a rounded appearance (Figures 80–84). In most Vandeae the pollinia in each set are fused (Table 2, t.s. 34) so that the sets look like spheres and there appear to be only two pollinia (Figures 80–83). In other Vandeae the fused sets are flat with a cleft delimiting the pollinia in each set (Figure 84).

2. Of all the orchids, only Spiranthinae and Cryptostylidinae (both are Cranichideae) and the Vandeae, Maxillarieae, Coelogyneae, and Malaxideae (all are Epidendroideae) have unequal sets of pollinia (Table 2, t.s. 33; Figures 38, 39).

3. The presence of cohesion strands is an apomorphic character (Table 2, t.s. 38) found in Spiranthoideae and Neottioideae. Cohesion strands are acetolysis-resistant structures and should not be confused with viscin strands that are performed sporopollenin threads. Unlike viscin strands, cohesion strands only assume their irregular shape after the pollen tetrads are pulled apart.

4. The presence of an operculate colpus is an apomorphic character (Table 2, t.s. 42) found in *Neuwiedia* (Newton and Williams, 1978; Schill, 1978) and *Apostasia* (Schill, 1978). We know of no other monocot group that possesses an operculum.

5. In Cypripedioideae, Orchidoideae, and most Epidendroideae the exine foot layer is absent, presumably through loss (Table 2, t.s. 40). Although the accompanying characters in each group indicate that the loss of the foot layer in these subfamilies are three different apomorphies, they were coded as the same because additional information on the pollen wall is still needed before we can be sure of their classification.

6. In the Cypripedioideae the loss of the foot layer is accompanied by the presence of incipient columellae (Table 2, t.s. 41), which is unique in the orchids and perhaps in the monocots (Burns-Balogh, 1983a).

CHARACTERS NOT USED IN THIS CLASSIFICATION

Exine sculpturing, vegetative characters such as leaf-type, root-stem tuberoids, corms, pseudobulbs, and perianth characters were not used in this cladistic study because they are inconsistent at the tribal level. Most of these characters have been used to define tribes or subfamilies in past classifications. The consistency of the pollen mass has also been used, especially by Lindley (1830–1840) and Schlechter (1911, 1926), but is an inconsistent character when used alone without the accessory structures. This reasoning also applies to the presence of nectaries and shape and size of the column foot. Most of these characters (or groups of characters) can be used at the generic level or below, but usually not at the subtribal, tribal, or subfamily levels. In addition, the presence of a labellum and the symmetry of the flower were not used as characters in this analysis because it was impossible to determine whether their presence was apomorphic or plesiomorphic in the Orchidaceae.

Cladogram Construction

The cladogram was constructed by parsimoniously arranging taxa so as to create the fewest number of character conflicts. The final cladogram was the one that required us to make the fewest number of ad hoc assumptions of parallel or convergent evolution or reversals. This procedure is called parsimony. The cladogram was constructed by examining a series of three taxon statements. The cladogram should be viewed as a hypothesis of relationships and not as "truth" or "fact." Cladograms produced by Hennig's method are direct reflections of the data; should the information change sufficiently, the cladogram will also change.

Discussion of Characters as Displayed on the Cladogram

Because the transformation series that contained more than one apomorphic character were coded in a conservative manner (apomorphic characters were treated as independent occurrences) we can now examine these apomorphies on the cladogram (Figure 1) and see if an alternative order is indicated (Table 4). One must be careful to treat these statements on the relationship of the apomorphies within the transformation series as hypotheses subject to change if and when additional information becomes available. In the following discussion of transformation series refer to Table 4.

T.S. 1.—All orchids have some fusion of the style and filaments. The partial fusion of the Neuwiedioid filaments and style can be considered independent of the anther fusion type or as a separate event. We have chosen to display it as one fusion series rather than have the initial fusion occur twice. From this partial fusion (1-1), first the style, filament, and staminode bases fused (1-2), then the style, filament, staminodes, and stigma fused to form the column (1-3, Area A). The two remaining apomorphies for this transformation series developed from the fused style/stigma/filament/staminodes. The transformation series has therefore been drawn to reflect this change.

T.S. 7.—The basal viscidium attachment can be interpreted as either developing once or twice from the apical attachment (Table 4). Both interpretations are equally parsimonious and give the same branching pattern. Although the former interpretation is the one indicated on the cladogram, we have no preference (Table 4).

T.S. 8.—The cladogram shows that the evolution of the rostellum is more complex than was originally coded (Table 4). Rather than each apomorphy being derived independently from three equally sized stigma lobes, the most parsimonious explanation is as follows: the apical stigma lobe developed in five independent directions, the strap-like rostellum of the Orchidoideae (8-2), the curled over one of the Epidendroideae (8-4), and the long rostellum of the Spiranthoideae (minus the Diurideae, 8-5). There was a parallel reduction of the rostellum (8-3) in the Diurideae (Spiranthoideae) and in the Neottioideae followed by a reversal to a rostellum longer than wide (8-5) in the Listerinae.

T.S. 14.—As was expected, character 14-2 is a synapomorphy for the monandrous orchids (Area A) and the Apostasioideae and Cypripedioideae are united by the synapomorphy of having only inner lateral stamens (14-3). The Neuwiedioideae, which have the plesiomorphic character of three stamens (14-1), are left out of either group.

T.S. 17.—The change in anther insertion on the filament could be sequential (Table 4) in that it progresses from inserted below the stigma (17-1) to at or near the stigma base (17-2; Area A) in the monandrous orchids, to at or near the stigma apex (17-3; Area B) and finally to above the stigma apex (17-4; Area C). In apomorphy 17-2 the anther parallels the stigma and in characters 17-3 and 17-4 the anther extends beyond the stigma apex. It would not change the branching sequence to interpret the apomorphies as independently derived, however, it would require repeated fusion of the same structures, so we prefer the sequential order.

T.S. 24.—When present, the inner lateral staminodes have one of eight apomorphies. The apomorphies were coded as independent and the cladogram supports this with the exception of inconspicuous staminodes (24-2) and the re-

TABLE 4.—Character relationships within selected transformation series as they were coded and after the cladogram was constructed.

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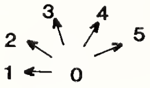
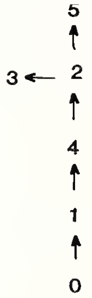
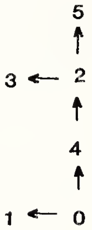
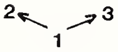
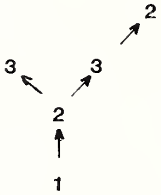
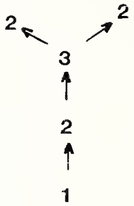
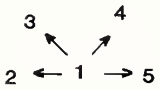
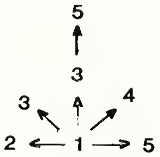
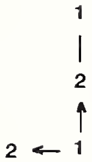
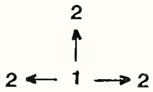
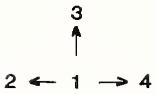
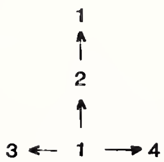
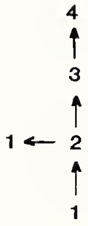
1		 or 
7		 or 
8		
13		 or 
17		 or 

TABLE 4.—*Continued.*

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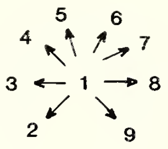
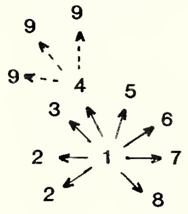
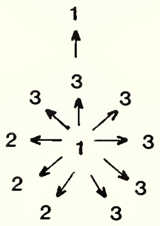
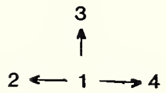
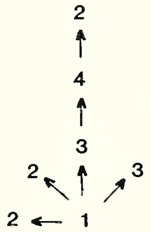
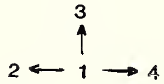
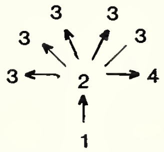
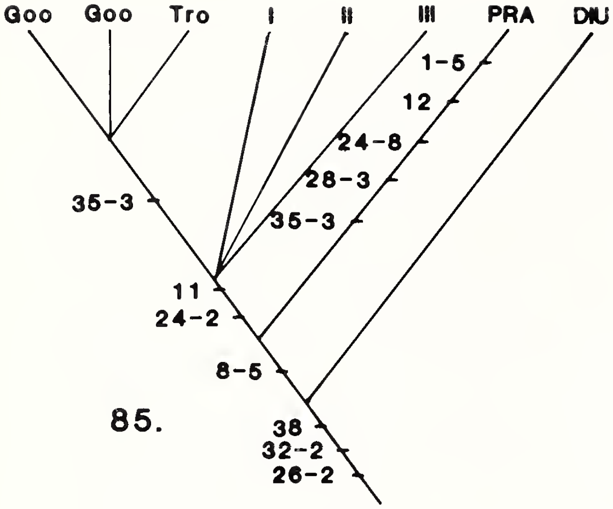
24		
28		
32		
35		

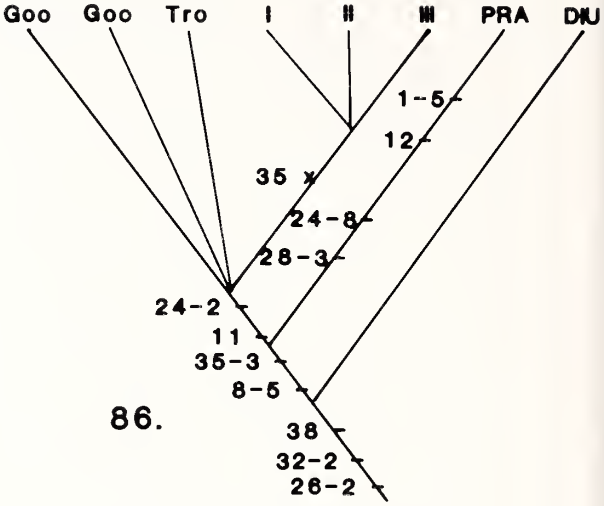
peated development of stamens fused to the column margins and cobra-hood-like above the anther (24-9) from a completely fused column structure (24-4).

T.S. 28.—In the Epidendroideae caudicles embedded with pollen (28-2) have occurred three times and sterile caudicles (28-3) twice. Sterile caudicles also characterize the Orchidoideae and many of the Spiranthoideae (minus the Diurideae). This is one of the most variable transformation series on the cladogram.

T.S. 32.—The pollinia shape can be interpreted as twice having developed a rounded base (32-2) and twice having developed a rounded



85.



86.

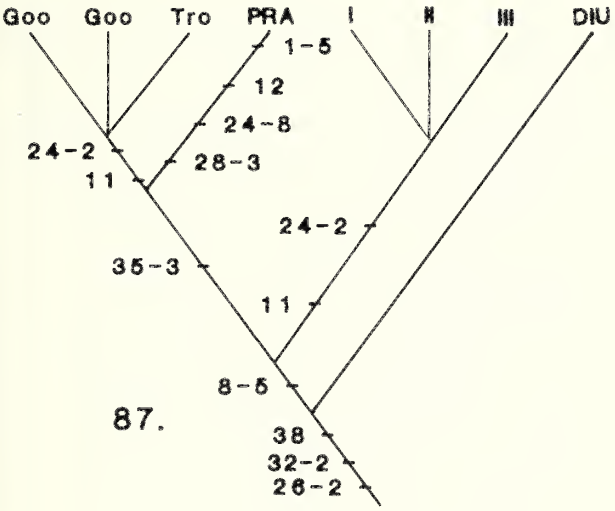
FIGURES 85-87.—Cladograms showing three possible groupings of taxa within the subfamily Spiranthoideae (only the characters important to this grouping question are illustrated—see Figure 1 and Table 3): 85, contains the hypothesis of homoplasy for character 35-3 (12 steps); 86, contains the hypothesis of reversal for character 35-3 (12 steps); 87, contains the hypotheses of homoplasy for characters 11 and 24-2 (13 steps) (Goo = Goodyeriana).

apex (32-3) from the primitive condition of both base and apex being attenuate. The rounded apex and base (32-4) developed from the round-attenuate condition once and from this the apex became rounded once again (Table 4).

T.S. 35.—Sectile pollen aggregation has developed five times from the granulate condition: (1) Orchidoideae, (2) Arethuseae (Epidendroideae), (3) Gastrodieae (Epidendroideae), (4) Goodyerinae-Tropidinae (Spiranthoideae), and (5) Prasophyllinae (Spiranthoideae), which makes this one of the most variable characters in this study.

Five multi-apomorphy transformation series were found to remain as they were originally coded. These are t.s. 14, 16, 19, 22, and 26.

Several transformation series with only one apomorphy showed some homoplasy (Figure 1). The one-chambered fruit (Table 2, t.s. 3; Figure 1) showed up in part of the Cypripedioideae and at Area A. The berry fruit (Table 2, t.s. 4; Figure 1) is in some Neuwiedioideae and in some Vanilleae. Stigma modification (Table 2, t.s. 6; Figure 1) is present in all of the Cypripedioideae and at Area A (monandrous orchids). The hamulus (Table 2, t.s. 12) appears three times in the Spiranthoideae and the tegulus (Table 2, t.s. 13) once in the Spiranthoideae and once in the Epidendroideae with a reversal in the Coelogyneae (Table 4). It is equally parsimonious to hypothesize that the tegular stipe developed three times but this assumption does not alter the branching sequence of the cladogram. Deciduous anthers (Table 2, t.s. 21; Figure 1) appear twice in the Epidendroideae. Tail-like caudicles (Table 2, t.s. 29; Figure 1) are characteristic of the Orchidoideae and some species of the Gastrodieae (Epidendroideae). Unequal pollinium sets (Table 2, t.s. 33) are found in two widely separated groups, the higher Epidendroideae and some species of the Cranichideae (Spiranthoideae). All monandrous orchids (Areas A-F of cladogram, Figure 1) have tetrad pollen units (Table 2, t.s. 36) except for some species of the Vanilleae (Epidendroideae), and in the taxa of the Neottioideae where it varies from monad to tetrad in every group. So variable is it in the Neottioideae that it is simply listed on the cladogram as 36-1/2. Cohesion strands (t.s. 38) are in both the Spiranthoideae and Neottioideae (see "Discussion of the



87.

Cladogram"). The lack of a foot layer (t.s. 40) occurs twice, the Cypripedioideae and Area C, but it reverses in the Vanilleae. The operculate colpus (t.s. 42) is found in the Neuwiedioideae and maybe Apostasioideae.

Transformation series with only one apomorphy that showed no homoplasy or reversals are as follows: 2, 5, 10, 15, 18, 20, 25, 30, 31, 34, 37, 39, and 41.

Based on the information gained by studying the cladogram the multi-apomorphic transformation series have been drawn to eliminate unnecessary reversals.

The characters that are shown to have evolved in parallel could be recoded as different characters. We have found them useful, however, when studying the pollination and ecology of various groups of orchids and prefer to leave them on the cladogram and merely indicate that they occur more than once by using a closed circle on the cladogram.

Discussion of the Cladogram and Resulting Classification

There are three areas on the cladogram that are very well defined by synapomorphies (Figure 1, Areas A, E, and F). One area delimits the monandrous orchids (Area A) with 10 synapomorphies. The recognition of the monandrous orchids as a unit, although usually an unnamed one (except at the family level), is not new as almost all orchidologists discuss this division. Few, if any, of the classifications of orchids have dealt with the differences in such an explicit manner and there are some surprises such as the presence of elastoviscin (Table 2, t.s. 37), anther base insertion (Table 2, t.s. 17), and staminode development (Table 2, t.s. 24).

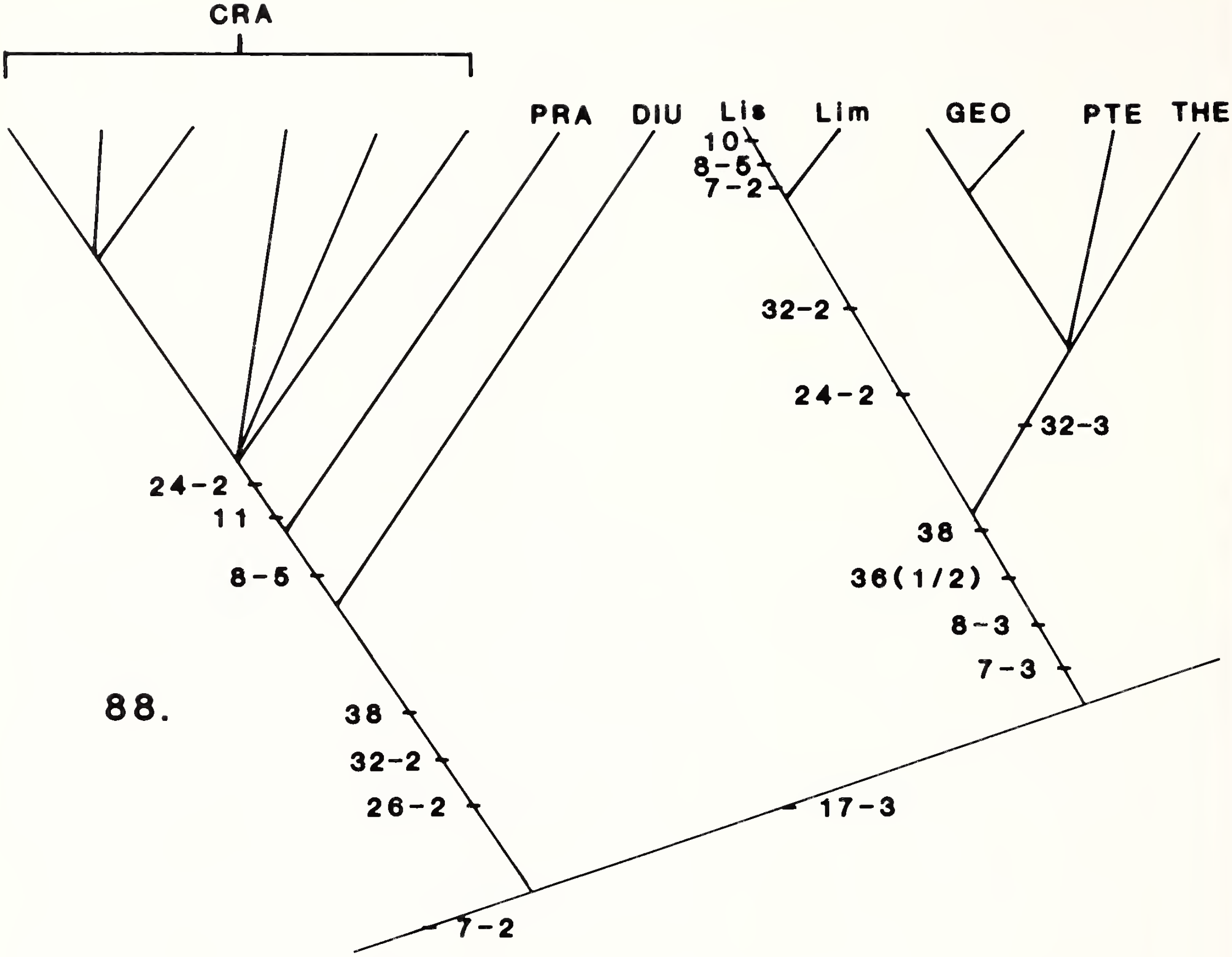
Area E is defined by five (sometimes six, see Table 2, t.s. 24-9) synapomorphies and separates all of the Epidendroideae except Gastrodieae and Triphoreae.

The third well-defined area, Area F, is somewhat of a surprise; although the Orchidoideae is a well known subfamily, there has been some discussion as to what does and does not belong in it. Because of the eight synapomorphies dealing with what are the most distinctive column and pollen characters in the family, it is easy to decide what should be considered part of this group. New characters include the presence of auricles (Table 2, t.s. 25).

Five other well-defined areas are apparent. Area D is defined by three synapomorphies and delimits the subfamily Epidendroideae. This is a well-established taxonomic group recognized by all workers in the family. All three of the characters, however, are new for the group while the traditional characters (hard, waxy pollen aggregation and incumbent anther) are apomorphies found in more restricted groups within the Epidendroideae.

Other areas of the cladogram that are well-defined are the subfamily Cypripedioideae with three synapomorphies, the "vandoid orchids" (Maxillarieae, Coelogyneae, and Vandeae of the Epidendroideae) and the Spiranthoideae and Apostasioideae with three synapomorphies each.

There are also areas that are less well-defined. The cladogram contains six polytomies, several weak dichotomies and one subfamily that is delimited only by characters that appear more than once on the cladogram. For instance, although

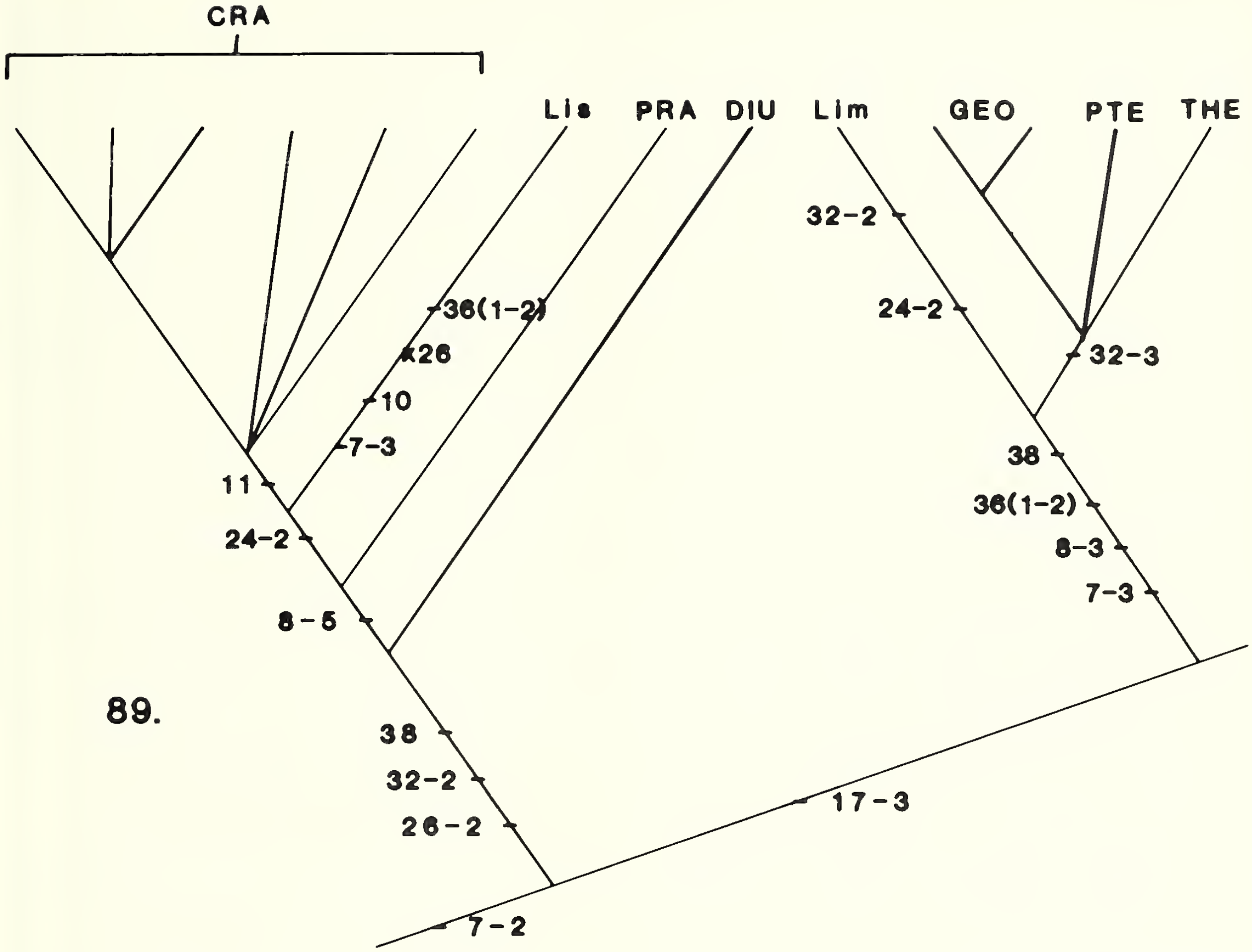


88.

FIGURES 88, 89.—Cladograms showing two possible groupings of the Listerinae (only the characters important to this grouping question are illustrated—see Figure 1 and Table 3): 88, Listerinae is grouped with the Neottioideae (18 steps); 89, Listerinae is grouped with the Spiranthoideae (19 steps).

the subfamily Epidendroideae is separated from the rest of the orchids easily (Area D), there are three polytomies and one tribe (Dendrobieae) that are not indicated to be monophyletic. This is a reflection of the poor understanding of the diversity of column characters within this subfamily.

The Spiranthoideae is more or less well-defined and the tribes Prasophylleae and Diurideae are strongly characterized, but the grouping within this subfamily is weak. There are three possible groupings of the subtribes (Figures 85–87); two of them are equally parsimonious (Figures 85, 86) and the third is only one step longer (Figure 87). Of the two critical characters (35-3 and 24-2), one (35-3) varies a great deal in the family (Table 4) and cannot be reliably used to group taxa. If we choose to group using character 24-2 then there are two equally parsimonious alternatives (Figures 85, 86) with the only difference being whether sectile pollen aggregation (35-3) developed twice within the subfamily (Fig-

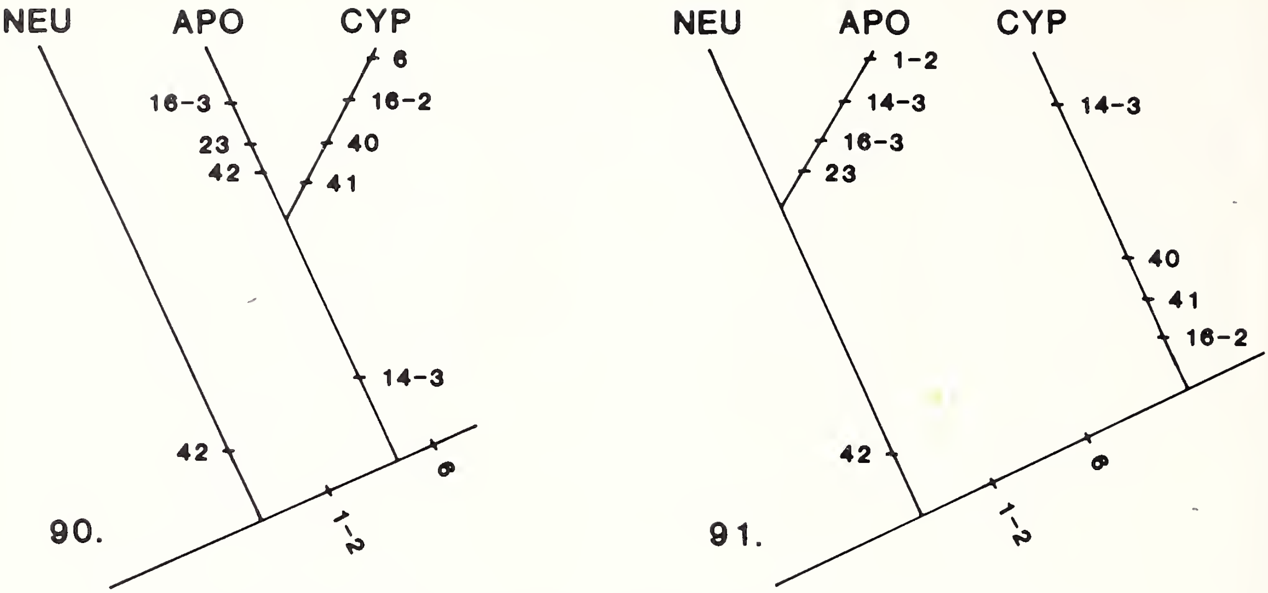


89.

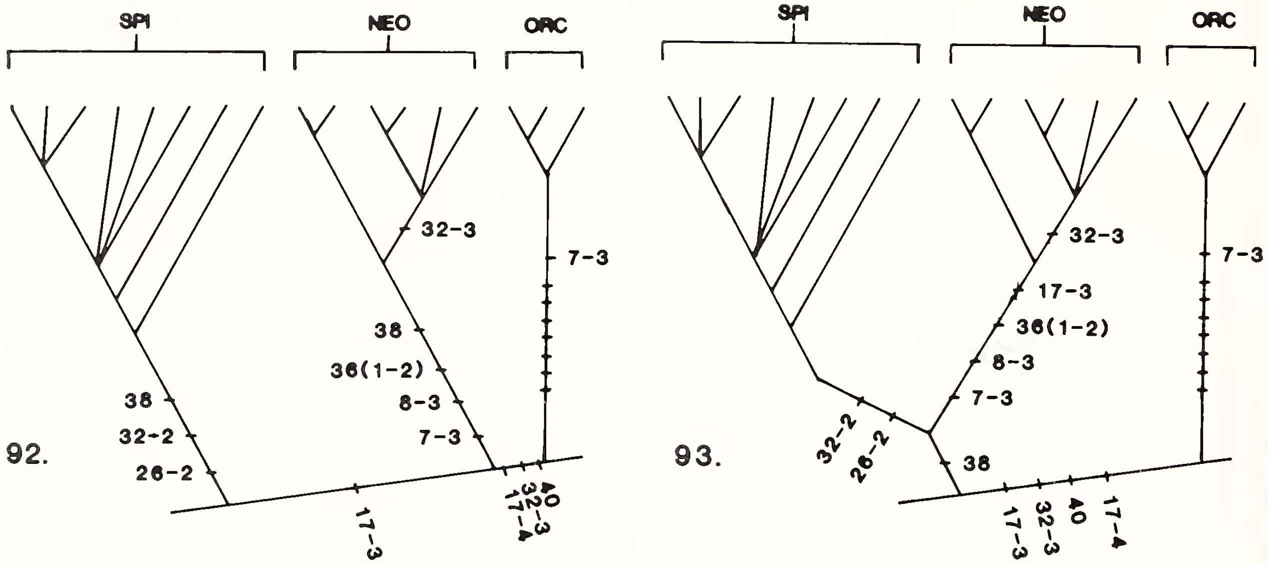
ure 85) or developed only once and then was lost (Figure 86). We think that at this time there is no reason to have a preference between these two cladograms. In addition, we have no indication that the Cranichis group (Cranichideae sensu Dressler) is monophyletic. Although both Goodyerinae I and Tropidinae have character 28-3 we have not grouped them together on the cladogram because this character is not believed to be homologous in the two groups; it is associated with different types of stipes. Because of the instability of the groupings within the Cranichideae we have refrained from making any nomenclatorial changes except for combining Dressler's Cranichideae and Erythrodeae under the name of the former.

Rasmussen (1982:81) suggested placing the Listerinae in the Cranichideae because they both have fascicled roots. We examined the possibility of such a relationship. Figures 88 and 89 show that based on our characters, such an arrangement would be less parsimonious.

Are the Apostasioideae more closely related to the Cypripedioideae than to the Neuwiedioideae? The two alternative arrangements are shown in Figures 90 and 91 and they indicate that both interpretations are equally parsimonious. The different arrangements depend on



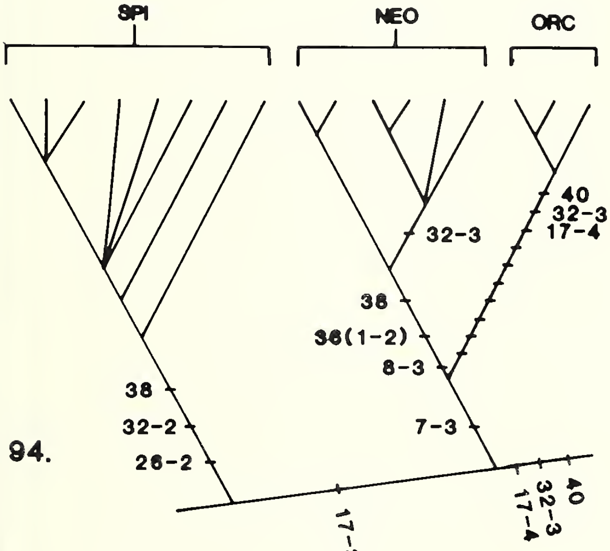
FIGURES 90, 91.—Cladograms showing two possible groupings of the Apostasioideae (only the characters important to this grouping question are illustrated—see Figure 1 and Table 3): 90, Apostasiodieae is more closely related to Cypripedioideae than to Neuwiedioideae (11 steps); 91, Apostasiodieae is more closely related to Neuwiedioideae than to Cypripedioideae (11 steps).



FIGURES 92–94.—Cladograms showing three possible groupings of the Neottioideae (only the characters important to this grouping question are illustrated; see Figure 1 and Table 3): 92, Neottioideae is the sister group of the Orchidoideae/Epidendroideae (20 steps); 93, Neottioideae is the sister group of the Spiranthoideae (20 steps); 94, Neottioideae is the sister group of the Orchidoideae (22 steps).

whether one wishes to postulate a parallel origin for the development of the outer median staminode (Table 2, t.s. 16) or for the operculate colpus (Table 2, t.s. 42). We have chosen to illustrate the Apostasioideae as more closely related to the Cypripedioideae than either is to the Neuwiedioideae because we have more confidence in the staminode character (Table 2, t.s. 16). We have not been able to find the operculate colpus (Table 2, t.s. 42) in *Apostasia* even though Schill (1978) reports that it exists. The Cypripedioideae appear to have an annulus which may represent a reduced operculum. Regardless of which pattern one prefers, it is obvious that the Apostasioideae are not as closely related to the genus *Neuwiedia* as has been indicated in past classifications where they were placed in the same subfamily.

Without a doubt, the most interesting area on the cladogram is the placement of the Neottioideae. There are three nearly equally parsimonious distributions of apomorphies. In one, the Neottioideae is positioned on the cladogram so that it is the sister group of the Orchidoideae/Epidendroideae (Figure 92). It can also be drawn as the sister group of the Spiranthoideae (Figure 93) with which it shares cohesion strands (character 38), and finally as the sister group of the Orchidoideae (Figure 94) with which it shares a basal viscidium attachment (character 7-3). The last one is two steps longer than the other two and is not considered further. Of the first two we have selected the first to use in our main diagram because it does not cause parallelisms in what appears to be a very stable character (Table 2, t.s. 17). However, the Neottioideae are still a definable group no matter which of the two most parsimonious cladograms one selects (Figures 92, 93). The possibility that they can be grouped in one of two ways merely emphasizes the need to recognize the Neottioideae as a separate subfamily. All of the defining characters of the Neottioideae are shared with either the Orchidoideae or the Spiranthoideae, or some section thereof, and one might be tempted to speculate on a hybrid origin for the Neottioideae involving the Orchidoideae and Spiranthoideae. However, hybridization occurs on the individual level and not on the subfamily level, so any hypothesis of hybridization would have to involve individuals and therefore cannot be addressed in this treatment.



94.

Should some groups within the Orchidaceae be recognized as separate families? For instance, Vermeulen (1966) recognized three families, Apostasiaceae, Cypripediaceae and Orchidaceae (monandrous orchids only), and Schlechter (1970–1984), two families, Apostasiaceae (including the Cypripedioideae) and Orchidaceae (monandrous orchids). Based on the cladogram there are three choices: all within one family; four families (Neuwiediaceae, Apostasiaceae, Cypripediaceae, and Orchidaceae—monandrous orchids); or three families (Neuwiediaceae, Apostasiaceae (diandrous orchids), and Orchidaceae (monandrous orchids). All of the groups are monophyletic and all are acceptable to most cladists. The goal of cladistic classification, however, is to achieve the maximum amount of information with the minimum amount of change. This goal can be rephrased as follows: maintain monophyletic groups while changing the existing nomenclature as little as possible. The second part of the goal applies to this situation. In order to justify a change in the current classification (and certainly one would have to be made because Neuwiedioideae would have to be recognized separately) the group or groups in question must be more closely related to something else than they are to the rest of the orchids. The three synapomorphies that unite all orchids indicate that all of the orchids are more closely related to one another than they are to anything else; therefore there is no information to be gained by breaking them up into separate families. It is our opinion that they should be maintained as a family.

Keys to the Subfamilies and Tribes of the Orchidaceae

Key to the Subfamilies

1. Anthers 2 or 3, base situated below stigma base; filaments and style fused only at base or filaments fused to style; pollen in monocolpate monads; stigma 3-lobed, situated between or above the anthers; labellum slightly zygomorphic or well developed 2
   2. Anthers 3, elongate; filaments and style fused only at base; . . . . **Neuwiedioideae**
   2. Anthers 2, short and broad; filaments fused to style; 3
      3. Staminode, if present, filament-like; stigmatic surface radial to slightly asymmetric; labellum slightly zygomorphic . . . . **Apostasioideae**
      3. Staminode large, well developed; stigmatic surface abaxial; labellum well developed . . . . **Cypripedioideae**
1. Anther 1, base situated at or near stigma base or at, near, or above stigma apex; filaments, style and stigma fused into a column; pollen mostly in monoporate tetrads, aggregated into pollinia; stigma 2- (rarely 3-) lobed, abaxial, third lobe modified into a rostellum; labellum usually well developed 4
   4. Anther parallel to stigma and rostellum; base positioned at or near stigma base; rostellum usually well developed and usually longer than broad (or reduced) . . . . **Spiranthoideae**
   4. Anther extending above stigma; base at or near or above stigma apex; rostellum as long as broad and curled over or strap-like or reduced (rarely absent) 5
      5. Anther base at or near stigma apex; rostellum reduced to absent or sensitive on contact, rarely longer than broad (Listerinae); pollinia granulate, in monads or tetrads . . . . **Neottioideae**
      5. Anther base above stigma; rostellum strap-like or curled over; pollinia sectile or hard and waxy (rarely granulate), in tetrads (rarely monads) 6
         6. Column erect or bending backwards; anther erect or at right angles to column or upside down, fused to column apex, locules

separated by a connective; pollinia sectile with elastoviscin caudicles . . . . **Orchidoideae**

6. Column erect or bending forward; anther incumbent and free (rarely suberect), locules covered by cap-like connective; pollinia usually hard and waxy (rarely sectile or granulate); often with accessory structures . . . . **Epidendroideae**

Keys to the Tribes

Spiranthoideae

1. Filament and style greatly reduced, stigma and anther free; rostellum highly reduced; staminodes free, long, thin; pollinium granulate . . . . **Diurideae**
1. Filament, style and stigma fused and not highly reduced; rostellum longer than wide; staminodes free or fused to sides of column; pollinia usually sectile 2
   2. Staminodes free, long, thick; caudicle reduced, sterile; stipe hamular; clinandrium incompletely fused . . . . **Prasophylleae**
   2. Staminodes fused to column and inconspicuous; caudicle reduced, sterile; stipe absent (except in Tropidinae); clinandrium completely fused . . . . **Cranichideae**

Neottioideae

1. Staminodes inconspicuous or absent; rostellum reduced, absent or sensitive . . . . **Neottieae**
1. Staminodes well-developed; rostellum reduced and usually removed with viscidium 2
   2. Column extremely reduced or absent; staminodes fused into a high collar-like structure; filament long and fused to inside of staminodal hood . . . . **Thelymitreae**
   2. Column long and well-developed; staminodes well-developed, broad and fused to sides of column; filament reduced 3
      3. Staminodes flared (resembling hood of cobra); stigma at apex of column . . . . **Geoblasteae**
      3. Staminodes wing-like; stigma midway down column . . . . **Pterostylideae**

Orchidoideae

1. Column erect; anther erect; stigma concave . . . . **Orchideae**
1. Column bending backward; anther upside down or at right angles to column; stigma not concave 2

2. Anther upside down and below stigma; column turned over at apex . . . . **Satyrieae**
2. Anther at right angles to stigma;* column bent over only at anther . . . . **Diseae**

Epidendroideae

1. Pollinia sectile 2
    2. Anther suberect . . . . **Gastrodieae**
    2. Anther incumbent . . . . **Arethuseae**
1. Pollinia granulate or hard and waxy 3
    3. Anther suberect . . . . **Triphoreae**
    3. Anther incumbent 4
        4. Pollinia granulate . . . . **Vanillieae** (also *Hexalectris* and *Sobralia* in the Epidendreae)
        4. Pollinia hard and waxy 5
            5. Caudicles as many as pollinia, embedded with pollen; viscidium semi-liquid or rarely solid . . . . **Epidendreae**
            5. Caudicles usually sterile or absent, if pollen embedded highly reduced or fused; viscidium absent or solid 6
                6. Pollinia with attenuate apex; viscidium solid . . . . Pleurothallis group . . . .
                6. Pollinia rounded, rarely attenuate, naked or with stipe; viscidium absent or solid 7
                    7. Pollinia naked, rarely with a hamular stipe (*Bulbophyllum*), and side by side 8
                        8. Pollinia in sets, equal . . . . **Dendrobieae**
                        8. Pollinia is sets, unequal . . . . **Malaxideae**
                    7. Pollinia with tegular stipe and sterile caudicle or fused pollen embedded caudicles with or without stipe, superposed 9
                        9. Caudicles fused, pollen embedded; with or without tegular stipe . . . . **Coelogyneae**
                        9. Caudicles free, sterile, reduced; with tegular stipe . . 10
                        10. Pollinia free in sets . . . . **Maxillarieae**
                        10. Pollinia fused in sets . . . . **Vandeae**

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* Dressler (pers. comm., 1983) notes that "*Disa* does not always seem to have an anther at right angles to the stigma."

Classification of the Orchidaceae

Non-Monandrous Orchids

NEUWIEDIOIDEAE Burns-Balogh and Funk, new subfamily

PLATE 1*a*

Anthereae tres, abaxiales, insertae infra stigma. Filamenta et stylus connati basi. Pollinis grana operculata.

Anthers 3, abaxial, representing outer median stamen and inner lateral stamens, free, elongate, base below stigma base; filaments long, fused at base to style. Pollen in monads, semi-tectate, with tectum, with columellae, foot layer present, operculate, monocolpate. Stigma lobes three, radially arranged, style equal to or longer than filaments. Perianth tubular, rudimentary nectar sac, median petal slightly irregular. Fruit a capsule or berry, 3-chambered, axile placentation.

TYPE.—*Neuwiedia* Blume in Hoeven and Vriese, Tijdschr. nat. geschied. I. 1834, p. 142.

DISTRIBUTION.—Malaysia.

TAXA.—1 genus with 10 species.

APOSTASIOIDEAE

PLATE 1*b*

Anthers 2, abaxial representing inner lateral stamens, broad, long, adherent at margins forming a tube around style, base below stigma base; filaments short, fused to style; staminode, when present, filament-like, adherent to anther margins. Pollen in monads, semi-tectate, with tectum, with columellae, foot layer present, operculate, monocolpate. Stigma 3-lobed, radially arranged, exserted; style longer than anthers. Perianth radiating, nectar sac absent, parts more or less similar. Fruit an elongate capsule, 3-chambered, axile placentation.

DISTRIBUTION.—Tropical Asia, Malaysia, Australia.

TAXA.—1 genus with ten species.

CYPRIPEDIOIDEAE

PLATES 1*c–e*, 3*a*

Anthers 2, abaxial, representing inner lateral stamens, separate at each side of column, rounded, base below stigma base; filaments short, fused to style; staminode large, well-developed; pollen in monads, mass sticky or powdery, tectate-imperforate, with incipient columellae, foot layer absent, monocolpate. Stigma 3-lobed, abaxial, facing towards labellum, longer than anthers, style thick. Perianth zygomorphic with well-developed labellum and nectary, outer lateral sepals often fused to form a flag-like structure above labellum. Fruit an elongate capsule, 3-chambered (*Selenipedium*, *Phragmipedium*) or 1-chambered (*Cypripedium*, *Paphiopedilum*), placentation axile or parietal.

DISTRIBUTION AND TAXA.—Four genera: *Cypripedium*: northern temperate, 50 species; *Phragmipedium*, tropical South America, 11 species; *Selenipedium*, tropical South America and West Indies, 3 species; *Paphiopedilum*, tropical Asia, 50 species.

Monandrous Orchids

Anthers 1, abaxial, representing median outer stamen, free or fused, elongate, parallel to or above stigma; filament with some portion of apex free or fused; staminodes 2, representing inner lateral stamens. Pollen in tetrads, rarely monads, united into masses called pollinia, exine various, pore one, proximal; with elastoviscin. Stigma fused to style and filaments to form a central column structure, lobes 2, some with a portion of third lobe also receptive; rostellum representing modified third stigma lobe (apical); viscidium present in most genera. Perianth zygomorphic, nectary usually present, labellum well-developed in most genera. Fruit an elongate capsule, ovary 1-chambered, placentation axile.

This study is only to the tribal level, though in some cases we have been able to define the subtribes also. For the most part our characters are apomorphic on the tribal level. Because of this most of the subtribes listed here are those of Dressler (1981).

SPIRANTHOIDEAE

Anther base situated at or near base of stigma, rarely near apex, free, erect to suberect, dorsal, parallel to stigmatic surface and rostellum; clinandrium well-developed, composed of the back of the stigma and margins of staminodes; staminodes inconspicuous and fused with column apex to well developed and free. Pollen in granulate or sectile masses, tetrads, cohesion strands, semitectate to tectate, foot layer, columellae, and tectum present. Stigma 2-lobed; rostellum erect to suberect, apical portion abscissing and forming the viscidium; viscidium mostly apical to rarely subapical depending on rostellum development; column foot rarely well developed. (See "Monandrous Orchids" for additional characters.)

DIURIDEAE

PLATE 1*f*

Staminodia membranous, free, prominent; clinandrium incompletely fused; pollinarium granulate, composed of monads (less often loosely aggregated tetrads); column absent or extremely reduced; stigma free, not fused to column, rostellum removed with viscidium portion; rootstem tuberoids.

DISTRIBUTION.—Australia.

TAXA.—2 genera (*Diuris*, *Orthoceras*); 40 species.

PRASOPHYLLEAE (Schlechter) Burns-Balogh and Funk, new status

PLATE 1*g*

Type: *Prasophyllum* R. Brown. Prodromus Florae Novae Hollandiae. 1810. p.317.—Staminodes free, long, thick; clinandrium incompletely fused; pollinia sectile, rarely granular, hamular stipe present, with reduced sterile caudicles; rostellum well-developed and longer than broad; flowers non-resupinate.

TYPE.—*Prasophyllum* R. Brown, Prodromus Florae Novae Hollandiae. 1810, p. 317.

DISTRIBUTION.—Australia, New Zealand.

TAXA.—1 genus with 40 species.

CRANICHIDEAE

PLATES 1*h–k*, 3*b–i*

Staminodes short and inconspicuous; clinandrium completely fused; pollinia sectile or granulate, with or without accessory structures; rostellum well-developed, longer than broad; flowers resupinate or non-resupinate.

TAXA.—7 subtribes.

GOODYERINAE

Tegular stipe and reduced sterile caudicle in some species; stems succulent trailing, rooting at the nodes. Three species of Goodyera have an incumbent anther above stigma.

DISTRIBUTION.—Mostly tropical but also temperate.

TAXA.—36 genera; 425 species.

TROPHIDINAE

Hamular stipe and reduced sterile caudicle present; sectile, rarely secondarily granulate pollinia; stems reed-like, leaves plicate.

DISTRIBUTION.—Pantropical.

TAXA.—2 genera; 12 species.

SPIRANTHINAE-I

Sterile caudicles rarely present; pollinia in unequal sets.

DISTRIBUTION.—Mostly tropical America.

TAXA.—17 genera; 325 species.

MANNIELLINAE-III

Staminodes prominent.

DISTRIBUTION.—Africa.

TAXA.—1 monotypic genus.

CRANICHIDINAE-II

Flowers non-resupinate; some with hamular stipe; pollinia round in cross section.

DISTRIBUTION.—Tropical and temperate areas.

TAXA.—15 genera; 200 species.

CRYPTOSTYLIDINAE-I

Pollinia in unequal sets.

DISTRIBUTION.—Australia and Asia.

TAXA.—1 genus with 15 species.

PACHYPLECTRONINAE-III

Staminodia web-like between stigma and anther margins.

DISTRIBUTION.—New Caledonia.

TAXA.—1 genus with 2 species.

NEOTTIOIDEAE

Anther base inserted at or near apex of stigma, free, erect to suberect or nodding, free, elongate; filament often bending over so anther appears terminal, free or fused to staminodes; pollen in granulate masses, monads or tetrads, with cohesion strands, semi-tectate to tectate, tectum, foot layer, and columellae present, with proximal or equatorial or distal pore. Stigma 2-lobed, usually concave in those with long column; rostellum short or extremely reduced or absent or sensitive; viscidium short and round or absent or semisolid; column foot not well-developed. (For additional characters, see section on "Monandrous Orchids," p. 53.)

TAXA.—4 tribes.

NEOTTIEAE

PLATE 3*j*

Staminodes reduced or absent; pollinium soft and mealy; rostellum, if present, greatly reduced or sensitive on contact.

TAXA.—2 subtribes.

LISTERINAE

Pollen grain pore distal or equatorial; rostellum sensitive, viscidium attachment above base of pollinia but rarely at apex; anther base in *Neottia* varies from near base of stigma to apex of stigma.

DISTRIBUTION.—North temperate.

TAXA.—2 genera; 38 species.

LIMODORINAE

Rostellum absent or reduced, when present viscidium basal or just above base; anther base varies in *Epipactis* from near base of stigma to apex of stigma.

DISTRIBUTION.—Australia, tropical Africa and Asia, and northern hemisphere.

TAXA.—5 genera including *Rhizanthella* and *Cryptanthemis*; 62 species.

THELYMITREAE

PLATE 1*m*

Staminodes fused into a high collar-like structure and fused to the filament; pollinium soft and mealy; column highly reduced, rostellum very short, viscidium solid.

DISTRIBUTION.—Malaysia, Australia, and New Zealand.

TAXA.—3 genera (*Thelymitra, Calochilus,* and *Epiblema*); 60 species.

GEOBLASTEAE

PLATE 1*l*

Staminodes broad and fused to sides of column forming a cobra-hood-like structure below and partially at base of anther and tapering to base of column, resembling some Epidendroideae; pollinia soft and mealy, rarely divided (*Caladenia*); column long and well-developed; rostellum reduced and usually removed with viscidium portion, viscidium solid to semi-solid.

TAXA.—2 subtribes.

CHLORAEINAE

DISTRIBUTION.—South America and New Caledonia.

TAXA.—6 genera; 100 species.

CALADENIINAE

DISTRIBUTION.—Australasian.

TAXA.—16 genera, 100 species.

PTEROSTYLIDEAE (Schlechter) Burns-Balogh and Funk, new status

Staminodes broad at apex and wing-like, tapering at base of column; pollinia soft and mealy; column long and well-developed; stigma separated from rostellum by long narrow sterile area, stigma oblong, positioned at ¼ to ¾ length of column; rostellum reduced and often removed with viscidium, viscidium semi-solid.

TYPE.—*Pterostylis* R. Brown, Prodromus Florae Novae Hollandiae. 1810, p. 326.

DISTRIBUTION.—Australasian.

TAXA.—1 genus with 70 species.

ANOMALOUS

Genoplesium, *Microtis* (hamular stipe); *Drakea*, *Spiculaea* (Drakaeinae?).

ORCHIDOIDEAE

Anther base inserted above stigma apex, fused to column apex, erect, inclined away from column axis, or bent backwards and upside-down, locules separated by anther connective; filament absent; clinandrium absent; staminodes with callus-like auricles. Pollen in tetrads united into massulae which are united by elastoviscin core threads; interlocular elastoviscin caudicles present on each pollinium set; pollen exine semitectate to intectate, foot layer absent, monoporate, proximal pore. Stigma 2-3 lobed, some on stigmaphores (Habenariinae), concave or protruding; rostellum strap-like at base, between anthers, often forming a bursicle; viscidium 1-2 parted; column foot absent. (For additional characterics see "Monandrous Orchids.")

TAXA.—3 tribes.

ORCHIDEAE

PLATES 1*n–p*, 2*a*, 3*k*

Anther erect; labellum often spurred.

TAXA.—3 subtribes.

ORCHIDINAE

DISTRIBUTION.—Mostly northern.

TAXA.—36 genera; 600 species.

HABENARIINAE

DISTRIBUTION.—Pantropical, Eurasia and Africa.

TAXA.—21 genera; 1100 species.

HUTTONAEINAE

DISTRIBUTION.—Southern Africa.

TAXA.—1 genus with 5 species.

SATYRIEAE

Anther upside down, bent backwards and below stigma; labellum double spurred.

DISTRIBUTION.—Mostly Africa.

TAXA.—3 genera; 110 species.

DISEAE

PLATE 2*b*

Anther at right angles to column, bending backwards; labellum not spurred; sepaline spur.

TAXA.—2 subtribes.

DISINAE

DISTRIBUTION.—Africa, especially southern Africa.

TAXA.—9 genera; 190 species.

CORYCIINAE

DISTRIBUTION.—Mostly Africa, but extending into tropical Asia.

EPIDENDROIDEAE

Anther situated above stigmatic surface, free, incumbent, rarely erect to suberect, with cap-like connective covering locules, locules usually 4 or divided into partitions; filament elastic or free and membranous or thick, or fused to column apex; clinandrium composed of dorsal (back) surface of rostellum and apex of column (with staminodes). Staminodes fused to column apex, some with free projections. Pollen in soft, mealy masses or hard, waxy spheres with or without accessory structures; exine semi-tectate to tectate, with or without foot layer, monoporate, with proximal pore. Stigma concave, tucked under rostellum, rarely protruding; rostellum broad and curled over, rarely erect, remnant often long and narrow; viscidium semi-liquid or solid or absent; column foot often well-developed. (For additional characters, see "Monandrous Orchids.")

TAXA.—10 tribes, 1 informal group (Pleurothallis).

GASTRODIEAE

Anther suberect; pollinia 4 in 2 sets, sectile, rarely secondarily granulate; pollen grain with or without foot layer to columellae, exine psilate to reticulate and no accessory structures (except Epipogoninae).

TAXA.—5 subtribes.

EPIPOGONINAE

With stipe and solid viscidium.

DISTRIBUTION.—Eurasia, tropical Africa, tropical Asia.

TAXA.—1 genus with 2–3 species.

GASTRODIINAE

DISTRIBUTION.—Pantropical, mostly tropical Asia and Australasia.

TAXA.—6 genera; 50 species.

STEREOSANDRINAE

DISTRIBUTION.—Eurasia.

TAXA.—1 genus with 2–3 species.

WULLSCHLAEGELIINAE

DISTRIBUTION.—Tropical America.

TAXA.—1 genus with 2 species.

NERVILIINAE

DISTRIBUTION.—Tropical Asia and Africa.

TAXA.—1 genus with 80 species.

TRIPHOREAE

Anther suberect, connective cap not well developed; pollinia 4, granulate, pollen grain exine reticulate, with or without foot layer, columellae absent; viscidium semi-liquid.

TAXA.—2 subtribes.

ACIANTHINAE

DISTRIBUTION.—Australasia.

TAXA.—4 genera; (?)100 species.

TRIPHORINAE

DISTRIBUTION.—Tropical America to North America.

TAXA.—3 genera; 20 species.

ARETHUSEAE

Anther incumbent; pollinia number (?), sectile; pollen grain exine psilate to coarsely reticulate, with or without foot layer; viscidium semi-liquid (?).

DISTRIBUTION.—North America.

TAXA.—1 monotypic genus.

VANILLIEAE

Anther incumbent; pollinia granulate, in monads or loosely aggregate tetrads, foot layer present; stigma with two flap-like lobes, viscidium semi-liquid.

TAXA.—4 subtribes.

VANILLINAE

Three chambered ovary in *Eriaxis* and *Vanilla*.

DISTRIBUTION.—Pantropics.

TAXA.—5 genera; 165 species.

PALMORCHIDINAE

DISTRIBUTION.—Tropical America and Africa.

TAXA.—2 genera; 12 species.

POGONIINAE

DISTRIBUTION.—Tropical and North America.

TAXA.—5 genera; 40 species.

LECANORCHIDINAE

Pollen polyporate.

DISTRIBUTION.—Tropical Asia.

TAXA.—1 genus with 20 species.

EPIDENDREAE

PLATES 2*c–e*, 3*l–m*

Anther incumbent; pollinia 4–8 with pollen embedded caudicles, pollinia side by side, rounded, more or less equal in size; viscidium semi-liquid to solid, foot layer absent.

TAXA.—3 subtribes.

BLETIINAE

DISTRIBUTION.—Mostly pantropical.

TAXA.—26 genera; 380 species.

SOBRALINAE

DISTRIBUTION.—Tropical America.

TAXA.—5 genera; 150 species.

LAELIINAE

DISTRIBUTION.—Tropical America.

TAXA.—43 genera; 830 species.

PLEUROTHALLIS Group

PLATES 2*f,g*, 3*n*, 4*a*

Anther incumbent; pollinia 2–8, with narrow attenuate apex, viscidium solid, foot layer absent.

TAXA.—6 subtribes.

PLEUROTHALLIDINAE

DISTRIBUTION.—Tropical America.

TAXA.—26 genera; 3800 species.

MEIRACYLLIINAE

DISTRIBUTION.—Tropical Mexico and Central America.

TAXA.—1 genus with 2 species.

PODOCHILINAE

DISTRIBUTION.—Australasia, tropical Asia and Africa.

TAXA.—7 genera; 230 species.

THELASIINAE

DISTRIBUTION.—Tropical Asia and Australia.

TAXA.—7 genera; 270 species.

ERIINAE

DISTRIBUTION.—Tropical Asia, Australia, and Africa.

TAXA.—8 genera; 500 species.

ADRORHIZINAE

DISTRIBUTION.—Tropical Asia.

TAXA.—2 genera; 3 species.

DENDROBIEAE

Anther incumbent; pollinia 4, naked, rarely with reduced pollen caudicles, waxy, pollinia side by side, adherent in sets, in more or less equal member sets, foot layer absent; elastoviscin between pollinia in sets; viscidium absent.

TAXA.—5 subtribes.

THUNIINAE

Pollinia eight.

DISTRIBUTION.—Tropical Asia.

TAXA.—6 genera; 42 species.

DENDROBIINAE

DISTRIBUTION.—Tropical Asia.

TAXA.—6 genera; 1650 species.

GLOMERINAE

Pollen embedded caudicles in some.

DISTRIBUTION.—Tropical Asia and Australia.

TAXA.—6 genera; 130 species.

SUNIPIINAE

Pollen embedded caudicles in some.

DISTRIBUTION.—Tropical Asia.

TAXA.—6 genera; 25 species.

BULBOPHYLLINAE

One species of *Bulbophyllum* with hamular stipe and reduced sterile caudicles.

DISTRIBUTION.—Pantropics.

TAXA.—7 genera; 1020 species.

MALAXIDEAE

Anther incumbent; pollinia 4, side by side, naked, in unequal sets, foot layer absent; viscidium semi-liquid.

DISTRIBUTION.—6 genera; 1890 species.

COELOGYNEAE

Anther incumbent; pollinia 4 in equal sets, superposed, with fused pollen caudicle and/or tegular stipe, foot layer absent; viscidium solid or semi-liquid.

TAXA.—2 subtribes.

COELOGYNINAE

Stipe absent.

DISTRIBUTION.—Tropical Asia.

TAXA.—4 genera; 440 species.

CORALLORHIZINAE

DISTRIBUTION.—North temperate and tropical America.

TAXA.—9 genera; 60 species.

MAXILLARIEAE

Anther incumbent; pollinia 4 in unequal sets, superposed, elastoviscin between pollinia, caudicle sterile, tegular stipe; viscidium solid.

TAXA.—10 subtribes.

CALYPSOINAE

DISTRIBUTION.—North America and eastern Asia.

TAXA.—2 genera; 3 species.

CRYPTARRHENINAE

Stipe absent.

DISTRIBUTION.—Tropical America.

TAXA.—1 genus with 3–4 species.

ZYGOPETALINAE

DISTRIBUTION.—Tropical America.

TAXA.—26 genera; 150 species.

BIFRENARIINAE

DISTRIBUTION.—Tropical America.

TAXA.—5 genera; 50 species.

LYCASTINAE

DISTRIBUTION.—Tropical America.

TAXA.—3 genera; 40 species.

MAXILLARIINAE

DISTRIBUTION.—Tropical America.

TAXA.—9 genera; 485 species.

DICHAEINAE

DISTRIBUTION.—Tropical America.

TAXA.—1 genus with 45 species.

TELIPOGONINAE

DISTRIBUTION.—Tropical America.
TAXA.—4 genera; 60 species.

ORNITHOCEPHALINAE

DISTRIBUTION.—Tropical America.
TAXA.—14 genera; 70 species.

POLYSTACHYINAE

DISTRIBUTION.—Pantropics, mostly Africa.
TAXA.—4 genera; 220 species.

VANDEAE

PLATES 2*h–n*, 4*b–k*

Anther incumbent; pollinia 4 in unequal sets superposed, fused (rarely free), foot layer absent, caudicle sterile, stipe tegular; viscidium solid.
TAXA.—11 subtribes.

SARCANTHINAE

DISTRIBUTION.—Tropical Asia, with a few species in Africa.
TAXA.—86 genera; 1000 species.

AERANGIDINAE

Double stipe in some.
DISTRIBUTION.—Tropical Africa.
TAXA.—34 genera; 300 species.

ANGRAECINAE

DISTRIBUTION.—Tropical Africa and tropical America.
TAXA.—16 genera; 400 species.

CYRTOPODIINAE

DISTRIBUTION.—Pantropical.
TAXA.—24 genera; 425 species.

GENYORCHIDINAE

DISTRIBUTION.—Tropical Africa.
TAXA.—1 genus with 6 species.

THECOSTELINAE

DISTRIBUTION.—Tropical Asia.
TAXA.—1 genus with 5 species.

CATASETINAE

Unisexual; pollinaria spring-ejected.
DISTRIBUTION.—Tropical America.
TAXA.—5 genera; 145 species.

ACRIOPSIDINAE

DISTRIBUTION.—Tropical Asia.
TAXA.—1 genus with 12 species.

STANHOPAEINAE

DISTRIBUTION.—Tropical America.
TAXA.—17 genera; 190 species.

PACHYPHYLLINAE

Double stipe in some.
DISTRIBUTION.—Tropical America.
TAXA.—2 genera; 25 species.

ONCIDIINAE

DISTRIBUTION.—Tropical America.
TAXA.—57 genera; 950 species.

Conclusion

Our system of classification follows the principles of phylogenetic systematics in that the emphasis is on the recognition and maintenance of monophyletic sister groups. We have used only characters that we found to be consistent at the tribal or subtribal level. Further, we have used only apomorphies to make groups (construct the cladogram). The resulting hierarchy is based on the cladogram and all recognized groups are monophyletic unless otherwise indicated.

Major points of comparison with other systems are as follows:

1. Our system differs from all others in the establishment of the subfamily Neuwiedioideae containing only the genus *Neuwiedia*.

2. The subfamily Spiranthoideae differs from that of Dressler in that we have transferred, as tribes, the Prasophyllinae (sensu Burns-Balogh, 1984c) and the Diurideae (sensu Burns-Balogh and Funk, 1984b) into this subfamily from the Orchidoideae (by Dressler, 1981).

3. Our concept of the Neottioideae is somewhat different from any other system in that we have transferred into it most of Dressler's Diurideae (except those referred to in no. 2 above) and the tribe Neottieae. We have resurrected Pfitzer's Thelymitreae with a single genus, and have raised the rank of the subtribe Pterostylidinae to tribal level. Caladeniinae and Chloraeinae have been combined into the Geoblasteae. Acianthinae, treated as a subtribe of Diurideae by Dressler, has been tentatively transferred to Triphoreae (Epidendroideae).

4. The tribes of the Epidendroideae presented some problems because of the lack of information on the column structure. However, several changes were made. The four tribes that remain similar to those of Dressler are Gastrodieae, Vanillieae, Malaxideae, and Dendrobieae. The Arethuseae, Triphoreae, Epidendreae, Pleurothallis Group, Coelogyneae, Maxillarieae, and Vandeae have been rearranged as far as contents of the subtribes. This is a tentative arrangement reflecting the information that was available for this study. Of all the areas on the cladogram we think these groupings have the greatest chance of changing as more information becomes available. The subtribes are those of Dressler. We could not cladistically demonstrate that four of these are monophyletic, however, because we have no synapomorphies for them (see Figure 1).

We feel that this classification is based on consistent characters and therefore reflects the natural groups within the Orchidaceae. However, we view this classification as a step in the direction of a phylogenetic classification because there are areas on the cladogram that lack resolution. Certainly, there is a need for specialists in the various groups to work within each tribe to determine the naturalness of the subtribes. New data in the form of additional synapomorphies or reinterpretation of the transformation series used in this study may indicate changes in this classification, especially in the subfamily Epidendroideae. One of the most advantangeous aspects of cladistic methodology is that it allows for easy criticism and reevaluation. We hope that this classification will provide the stimulation for those who both agree and disagree with our method and results to provide additional information to test our classification.

APPENDIX

List of Specimens Examined

The data in this section are presented by subfamilies. The species name is followed by the collector's name and number. The herbarium or collection where the specimen is housed and the collection number, when available, are given in parentheses. Abbreviations are as follows: AMO = Associacion Mexicana de Orquideologia; NYS = New York State Museum, Albany, NY.; SI = U.S. National Orchid Collection, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; SEL = Marie Selby Botanical Garden Greenhouse; NCBG = National Captial Botanical Garden Greenhouse, Canberra; s.n. = sine numero (without number). These greenhouse plants often had no collector or collecting number. If the abbreviation is followed by a number, then it indicates the greenhouse identification number and not the collecting number. Balogh = preserved material held in Balogh's personal collection.

APOSTASIOIDEAE.—*Apostasia* sp., Booea 7683 (US); *A. wallichii*, Brass 25570 (US), Booea 7808 (US).

NEUWIEDIOIDEAE.—*Neuwiedia zollingeri*, Booea 7949 (US); *N. veratifolia*, Booea 8991 (US); *N. griffithii*, Bartlett 6421 (US), Yates 2258 (US).

CYPRIPEDIOIDEAE.—*Cypripedium acaule*, Balogh 1053 (US); *C. xmontanum*, Balogh 1059 (US); *C. pubescens*, Dressler s.n. (Balogh). *Paphiopedilum glaucophyllum* (SI 781862, SEL 1-75-77); *P. exul* (SI 781138); *P. maudiae*, cultivated (Balogh); *P. spicerianum* (SI 781081). *Phragmipedium caricinum* (SI 78431); *P. longifolium*, Dressler s.n. (Balogh), Dodson s.n. (SEL); *P. schlimi*, Mejia s.n. (Balogh). *Selenipedium chica*, Dressler s.n. (Balogh).

SPIRANTHOIDEAE.—*Altensteinia fimbriata*, Barriga 7769 (US). *Anoectochilus regalis*, Jayasuriya 1219 (US).

Baskervillea paraensis, Handro 2256 (US). *Beloglottis costaricensis*, Greenwood 858 (AMO). *Brachystele affinis*, Greenwood 865 (AMO); *B. polyanthus*, Greenwood 2 (AMO), 841 (AMO).

Cheirostylis gymnochiloides, Humbert 17794 (US); *C. longilora*, Smith 1628 (US). *Corymborkis flava*, Killip and Hazen 8982 (US); *C. forcipigera*, Turckheim 860 (US). *Cranichis apiculata*, Greenwood 793 (AMO); *C. cililabia*, Greenwood 783 (AMO); *C. cucullata*, Greenwood 825 (AMO); *C. subumbellata*, Suarez 92 (US). *Cryptostylis subulata*, Bernhardt s.n. (Balogh). *Cyclopogon congestus*, Regnell 1197 (US); *C. elatus*, Greenwood 519 (AMO); *C. millei*, Luer 2414 (SEL); *C. saccatus*, Arsene 5152 (US); *C.* sp., Foster s.n. (US).

Deiregyne hemichrea, Greenwood 752 (AMO), Hagsater s.n. (AMO); *D. obtusa*, Greenwood 321 (AMO); *D. pulchra*, Greenwood 407 (AMO); *D. pyramidalis*, Greenwood 798 (AMO), Balogh 1019 (US); *D. tenuiflora*, Greenwood s.n. (AMO), *Dichromanthus cinnabarinus*, Greenwood 990 (AMO), Balogh 723 (US). *Diuris aurea*, Clements 2384 (NCBG), *D. longifolia*, Clements 2108 (NCBG); *D. maculata*, Bernhardt s.n. (Balogh), Clements 2388 (NCBG); *D. sulphurea*, Clements 2389 (NCBG).

Erythrodes sp., Foster s.n. (Balogh); *E.* sp., Dressler 4675 (US); *E. hyphaenctica*, Dodson s.n. (SEL); *E. maculata* (SEL 81-1771); *E. procera*, Abbott 2705 (US). *Eurystyles* sp., Kuhn s.n. (SEL).

Gomphicus viscosa, Wurdack 1734 (US). *Goodyera oblongifolia*, Balogh 1055 (US); *G. pubescens*, Balogh 907 (US).

Hetaeria oblongifolia, Merrill 4026 (US).

Ligeophila jamesonii, Dodson s.n. (SEL); *L. stigmatoptera*, Fernandez 2141 (US). *Ludisia discolor*, cultivated (Balogh).

Manniella gustavi, Tryon 6485 (AMES). *Macodes anderiana* (SI 781346).

Pachyplectron neocaledonia, McPherson s.n. (Balogh). *Pelexia funckiana*, Balogh and Greenwood 959 (US), Behib 707 (Balogh); *P. laxa*, Balogh s.n. (Balogh). *Physurus sagreanus*, Jimenez 2757 (US). *Platythelys* sp., Dressler s.n. (Balogh). *Ponthieva* sp., Greenwood 994 (AMO); *P. maculata*, Greenwood 1008 (US); *P. racemosa*, Greenwood 1020 (AMO); *P. tuerkheimii*, Greenwood 1006 (AMO). *Prasophyllum* sp., Clements 2111 (NCBG); *P. alpinum*, JT 1275 (NCBG); *P. densum*, Clements 2319 (NCBG); *P. elatum*, Clements (NCBG); *P. fimbriatum*, Clements 2301 (NCBG); *P. macrostachyum*, George s.n. (Balogh); *P. morrisii*, Clements 2316 (NCBG); *P. nublingii*, SH 1147 (Balogh); *P. rufum*, Clements 2318 (NCBG); *P. ruppii*, Clements 2298 (NCBG); *P. suttonii*, JT 1340 (Balogh); *P. woolsii*, Clements 2312 (NCBG). *Prescottia stachyoides*, Dressler s.n. (Balogh); *P. tubulosa*, Greenwood 922 (AMO). *Pterichis triloba*, Ferreyra 7534 (US).

Sarcoglottis sp., Greenwood 915 (AMO); *S.* sp., Greenwood 657 (AMO); *S.* sp., Greenwood 915 (AMO); *S. sp.*,Greenwood 657 (AMO); *S.* sp., Greenwood 352 (AMO); *S.* sp., Greenwood 757 (AMO); *S. acaulis*, Greenwood 657 (AMO); *S. cerina*, Dix 785 (Balogh); *S. gutturosa*, Greenwood 722 (AMO); *S. rosulata*, Greenwood 450 (AMO); *S. schaffneri*, Hagsater 5458 (AMO), Greenwood 1023 (AMO). *Schiedeella chloraeformis*, Greenwood 317 (AMO); *S. densiflora*, Greenwood 1011 (AMO); *S. eriophora*, Balogh 1011 (US), Greenwood s.n. (AMO); *S. falcata*, Balogh 969 (US); *S. hyemalis*, Hagsater 5739 (AMO); *S. llaveana*, Balogh and Greenwood 924 (US), Greenwood 930 (AMO); *S. michuacana*, Greenwood 813 (AMO); *S. pseudopyramidalis*, Balogh and Greenwood 917 (US); *S. saltensis*, Greenwood 860 (AMO). *Solenocentrum costaricensis*, Dressler 5841 (Balogh). *Spiranthes cernua*, Balogh 914 (US), Sheviak 1695 (NYS); *S. lacera*, Balogh 904 (US); *S. ochroleuca*, Balogh 913 (US), Sheviak 1657 (NYS); *S. praecox*, Grelen s.n. (Balogh); *S. romanzoffiana*, Pierce 911 (Balogh). *Stenoptera pilifera*, Haught 3315 (US). *Stenorrhynchos arechavaletanii*, Smith and Klein 12217 (US); *S. aurantiacus*, Balogh 735 (US); *S. balanophorostachys*, Gehrt (US); *S. canterae*, Herter 9878 (US); *S. cuspidata*, Dodson s.n. (SEL); *S. densus*, Hatschbach 26598 (US); *S. lanceolatus*, Greenwood 393 (AMO), Balogh 723 (US); *S. lateritus*, Hoehne and Gehrt (US); *S. regius*, Macedo 2667 (US); *S. speciosus*, Greenwood 518 (AMO); *Tropidia angulosa*, Henry 1905 (US).

Vrydagzynea micronesiaca, Glassman 2860 (US).

Zeuxine stricta, Smith 8457 (US).

NEOTTIOIDEAE.—*Aphyllorchis pallida*, Clements 323 (US). *Asarca sinuata*, Senn 4277 (US); *A. patagonica*, Joseph 1072 (US).

Caladenia angustata, Bernhardt s.n. (Balogh); *C. angustifolia*, Bernhardt s.n. (Balogh); *C. cairnsiana*, Clements 2183 (Balogh); *C. catenata*, Clements s.n. (NCBG), Rogers s.n. (Balogh); *C. caerulea*, Bernhardt s.n. (Balogh); *C. deformis*, Bernhardt s.n. (Balogh); *C. dilatata*, Clements 2107 (NCBG), Kelly, s.n. (Balogh) *C. doutchae*, Clements 2099 (NCBG); *C. filamentosa*, Clements 2102 (NCBG), Bernhardt s.n. (Balogh); *C. graminifolia*, Clements 2103 (NCBG); *C. flava*, Clements 2100 (NCBG); *C. latifolia*, Clements 2105 (NCBG); *C. patersonii*, Bernhardt s.n. (Balogh); *C. reticulata*, Bernhardt s.n. (Balogh); *Caleana minor*, Matthews s.n. (US). *Calochilus campestris*, Clements 2386 (NCBG); *C. robertsonii*, Bernhardt s.n. (Balogh); Kelly s.n. (Balogh). *Cephalanthera oregana* (austinae), Sandberg and Leiberg 571 (US); *C. rubra*, Podpera 21 (US); *C. grandiflora*, Cintract 1886 (US). *Chiloglottis gunnii*, Bernhardt s.n. (Balogh). *Chloraea crispa*, White s.n. (US); *C.* sp., Piquilieu 3745 (US); *C. nudilabia*, Hutchison 297 (US). *Codonorchis lessonii*, Goodall 433 (US).

Elythranthera brunonis, Clements (NCBG). *Epiblema grandiflora*, Pritzel 100 (US). *Epipactis gigantea*, Hall 2370 (US), Heller and Kennedy 8871 (US), *E. palustris*, Kurzweil s.n. (Balogh), *E. atrorubens*, Stephanoff and Georgieff (US).

Eriochilus cucullatus, SH 1146 (Balogh), Bernhardt s.n. (Balogh); *E. fimbriatus*, French s.n. (US).

Genoplesium baueri, Clements 2305 (NCBG). *Glossodia major*, Mueller s.n. (US), Clements 2348 (NCBG), Bernhardt s.n. (Balogh); *G. minor*, Boorman s.n. (US).

Limodorum abortivum, Franchschi 343 (US). *Listera auriculata*, Fernald and Collins 200 (US); *L. borealis*, Calder and Savile 9939 (US); *L. caurina*, Parks and Tracy 11667 (US); *L. ovata*, Kurzweil s.n. (Balogh).

Megastylis gigas, Mckee 7755 (US), Buchholz 1186 (US). *Microtis alba*, Pritzel 922 (US); *M. parviflora*, Bernhardt s.n. (Balogh); *M. uniflora*, Fosberg 30757 (US).

Neottia nidus-avis, Fosberg 35805 (US).

Pterostylis baptistii, Bernhardt s.n. (Balogh); *P. cucullata*, Clements s.n. (NCBG); *P. decurva*, Bernhardt s.n. (Balogh); *P. foliata*, Allison s.n. (US); *P. nana*, Bernhardt s.n. (Balogh); *P. nutans*, Bernhardt s.n. (Balogh); *P. obtusa*, Bernhardt s.n. (Balogh); *P. parviflora*, Clements 2307 (NCBG); *P. pulchella*, Clements 2321 (NCBG); *P. revoluta*, SH 1160 (Balogh); *P. rufa*, Clements s.n. (NCBG); *P. truncata*, Bernhardt s.n. (Balogh).

Rhizanthella gardneri, George 15717, McGuiness s.n. (US).

Thelymitra antennifera, Bernhardt s.n. (Balogh); *T. carnea*, Clements 2383 (NCBG); *T. media*, Bernhardt s.n. (Balogh); *T. nuda*, Clements (NCBG), *T. pauciflora*, Bernhardt s.n. (Balogh), Kelly s.n. (Balogh).

ORCHIDOIDEAE: *Aceras anthrophorum*, Dressler s.n. (Frankfurt Botanical Garden). *Amerorchis rotundifolia*, Sandberg 1014 (US). *Anacamptis pyramidalis*, Fosberg 32759 (US), Castella 1886 (US).

Brachycorythis pubescens, Leipoldi s.n. (US), Wood s.n. (US). *Brownleea caerulea*, Kemp 771 (US).

Ceratandra bicolor, Schlechter 9296 (US). *Chamorchis alpina*, Fosberg 33093 (US), Aryet 9800 (US), Kurzweil s.n. (Balogh). *Coeloglossum viride*, Larsen 20867 (US). *Corycium nigrescens*, Bayliss (US). *Cynorchis angustipetala*, Decary 6159 (US).

Dactylorhiza aristata, Murie 6 (US); *D. incarnata*, Kurzweil s.n. (Balogh). *Disa bivalvata*, Kemp 771 (US), Fourcave 529 (US); *D. cornuta*, Wright 131 (US); *D. crassicornis*, Wood 8430 (US). *Disperis* sp., Ramoorthy 1920 (US), *D. cooperi*, Wood 8096 (US).

Galearis spectabilis, Balogh 907 (US). *Gymnadenia odoratissima*, Kurzweil s.n. (Balogh).

Habenaria alata, Greenwood 576 (US); *H. clypeata*, Greenwood 917 (AMO); *H. dilatata*, Balogh 1058 (US); *H. distans*, Greenwood 720 (AMO); *H. genuflexa*, Kurzweil s.n. (Balogh); *H. guadalajarana*, Greenwood 700 (AMO); *H. longiauriculata*, Kurzweil s.n. (Balogh); *H. macroceratitus*, Greenwood s.n. (AMO); *H. novemfida*, Greenwood 891 (AMO); *H. odontopetala*, Greenwood 532 (AMO); *H. oreophila*, Greenwood 798 (AMO); *H. trifida*, Greenwood 719 (AMO); *H.* sp., Balogh 750 (US). *Herminium monorchis*, Kurzweil s.n. (Balogh). *Herschelia homalopetala*, Stolz 127 (US). *Himantoglossum hircinum*, Dvorak and Novacek 197 (US). *Holothrix praecox*, Tebrum 7850 (US). *Huttonea fimbriata*, (US 266172).

Nigritella nigra, Kurzweil s.n. (Balogh).

Ophrys cornuta, Reichenger s.n. (US); *O. fusca*, Lager s.n. (US); *O. morio*, Kurzweil s.n. (Balogh); *O. rotundifolia*, Dike s.n. (US); *O. ustulata*, Kurzweil s.n. (Balogh); *Orchis coriophora*, Kurzweil s.n. (Balogh).

Peristylus plantagineus, Ramamoorthy 2008 (US). *Perularia fuscescens*, Bach s.n. (US); *P. ussuriensis*, Matsuki 342 (US).

Piperia unalasensis, Balogh 1056 (US).

Platanthera sp., Greenwood 904 (AMO); *P. nivea*, Balogh 1066 (US); *P. ciliaris*, Zaret s.n. (MARY). *Pterygodium catholicum*, Robyns 17938 (US).

Satyrium coriifolium, Clements s.n. (NCBG); *S. mairei*, Rock 16913 (US); *S. nepalense*, Schneider 2981 (US). *Schizochilus sandersonii*, Bayliss 2541 (US). *Serapias cordigera, Teles and Rainka* 331 (US); *S. parviflora*, Kurzweil s.n. (Balogh). *Stenoglottis fimbriata*, Lodd 6975 (US); *S. longifolia*, cultivated (Balogh).

Traunsteinera globosa, Kurzweil s.n. (Balogh).

EPIDENDROIDEAE.—Epidendroid: *Acianthus* *exsertus*, Bernhardt s.n. (Balogh); *A. fornicatus*, (Canberra Botanical Garden); *A. reniformis*, Gunn 189 (US). *Acostaea unicornuta*, Luer 760 (SEL). *Adrorhiza purpurascens*, Jayasuriya and Balasubramanium 1228 (US). *Aglossorhyncha jabiensis*, Dressler s.n. (Balogh). *Agrostophyllum aseki*, Dressler s.n. (Balogh); *A. majus*, Dressler s.n. (Balogh). *Alamania punicea*, Greenwood s.n. (AMO); *Amblostoma tridactylum* (SI 7818). *Appendicula cornuta*, Dressler s.n. (Balogh). *Arethusa bulbosa*, Cheney s.n. (US). *Arpophyllum* sp., Hagsater 4502 (AMO), Greenwood 412 (AMO); *A. giganteum*, Suarez 171 (AMO). *Artorima erubescens*, Lamas s.n. (Balogh). *Arundina graminifolia*, Dressler s.n. (Balogh).

Barkeria cyclotella (SI 781184); *B.melanocaulon*, MacDougall s.n. (Balogh); *B. vanneriana*, Greenwood s.n. (AMO). *Bletia* sp., Greenwood 1093 (AMO); *B. ensifolia*, Greenwood 1035 (AMO); *B. liliacina*, Greenwood 1094 (AMO); *B. purpurea*, Balogh 962 (US); *B. reflexa*, Suarez (AMO); *B. roezlii*, Balogh 744 (US); Greenwood 1033 (AMO). *Bletilla striata*, cultivated (Balogh). *Brassavola nodosa*, cultivated (Balogh). *Broughtonia sanguinea*, (SI 781196). *Bulbophyllum baileyi*, SH 1138 (Balogh); *B. exiguum*, Clements 2308 (NCBG); *B.* sp., (SI 79800).

Cadetia sp., (SEL-77-2788). *Calanthe* sp., Dressler s.n. (Balogh); *C. brevicornu*, Dressler s.n. (Balogh); *C. rubens*, cultivated (Balogh).

Calopogon multiflorus, Curtiss 2802 (US).

Calypso borealis, Sandberg 93 (US); *C. bulbosa*, Peterson (Balogh). *Cattleya* sp., (SI); *C. aurantica*, Greenwood (AMO); *C. bowringiana*, (SI 76563); *C. skinneri*, Pollard (AMO). *Ceratostylis rubra* (SI 7883). *Chysis maculata*, Dressler s.n. (Balogh). *Cirrhopetalum collettii*, cultivated (Balogh); *C. elatum* (SEL 883). *Cleistes divaricata*, Chapman s.n. (US); *C. rosea*, Dressler s.n. (Balogh). *Coelia bella*, Greenwood 540 (AMO); *C. guatemalensis*, Greenwood 658 (AMO). *Coelogyne graminifolia*, Dressler s.n. (Balogh); *C. mayeriana*, (SEL); *C. pandurata* (SI); *C. virescens* (SI). *Corybas fimbriatus*, (NCBG 761061); *Corybas prunosus*, Bernhardt s.n. (Balogh). *Cryptarrhena guatemalensis*, Dressler 3550 (Balogh); *C. lunata*, Dressler s.n. (Balogh). *Cryptophoranthus beloglottis*, (SEL 5-75-11); *C. tribuloides*, Suarez (AMO).

Dendrobium aggregatum, cultivated (Balogh); *D. antennatum* (SEL); *D. bullenianum* (SEL 23-74-561); *D. delacourii* (SI 76400); *D. discolor*, Bernhardt s.n. (Balogh); *D. macbrownii*, SH 1145 (Balogh); *D. mijakei* (SI 792139); *D. pierardii*, cultivated (Balogh); *D. ruppianum*, Clements 2342 (NCBG); *D. secundum* (SEL); *D. tozerensis*, SH 1141 (Balogh). *Dendrochilum glumaceum*, cultivated (Balogh); *D. insectifera*, Robinson and Klass (US). *Dichaea morrisii*, Dressler s.n. (Balogh); *D. panamense*, Dressler s.n. (Balogh). *Dilochia cantleyi*, Dressler s.n. (Balogh). *Dimeranda emarginata* (SI 791071). *Dresslerella pertusa*, Dressler s.n. (SEL).

Elleanthus sp. (SI 81064); *E. capitatus*, Dressler 4061 (Balogh); *E. trilobatus*, (SI 791875). *Encyclia asperula*, Dressler and Pollard s.n. (AMO); *E. citrina*, Greenwood 987 (AMO); *E. cochleata*, Balogh s.n. (US); *E. candollii*, Balogh 1063 (US); *E. livida*, Balogh 795 (US); *E. pentotis*, Dressler s.n. (Balogh); *E. pollardiana*, Greenwood 687 (AMO); *E. pterocarpum*, Hagsater s.n. (AMO); *E. tampense*, Balogh (US); *E. tripunctata*, Balogh s.n. (Balogh); *E. vespa*, Balogh s.n. (Balogh). *Epidanthus paranthicus*, Hagsater 5671 (AMO). *Epidendrum acunae*, Hagsater 2073 (AMO); *E. alfaroi*, Dressler 5343 (Balogh); *E. anisatum*, Hagsater 5473 (AMO); *E. anoglossum*, Hagsater 6344 (AMO); *E. barbeyanum*, Hagsater 5643 (AMO); *E. bifalce*, Hagsater 5910 (AMO); *E. bisulcatum*, Hagsater 6457 (AMO); *E. brateosum*, Hagsater 6357 (AMO); *E. brownoides* (SI); *E. cerinum*, Hagsater 5776 (AMO); *E. ciliare* (SI, SEL); *E. clowesii*, Behib 702; *E. cnemidophorum*, Hagsater 4305 (AMO); *E. conopseum*, Balogh 720 (US); *E. corrifolium* (Stenoglossum), Dressler s.n. (Balogh); *E. costatum*, Hagsater 4303 (AMO); *E. curvicolumna*, Hagsater 6520 (AMO); *E. difforme*, Hagsater 4670 (AMO); *E. diffusum*, Hagsater 6101 (AMO); *E. eximium*, Dix 200876 (Balogh); *E. floribundum*, Hagsater 5902 (AMO); *E. gregorio*, Hagsater 6410 (AMO); *E. ilense* (SEL); *E. incomptum*, Hagsater s.n. (AMO); *E. juergensenii*, Hagsater 4299 (AMO); *E. jejunum*, Hagsater 6062 (AMO); *E. latilabrum*, Hagsater 6390 (AMO); *E. latifolium*, Hagsater 5228 (AMO); *E. laucheanum*, Hagsater 6121 (AMO); *E. longicaule*, Hagsater 6634 (AMO); *E. magnificum*, Hagsater 2600 (AMO); *E. marmoratum*, Hagsater 6043 (AMO); *E. morganii*, Hagsater 6586 (AMO); *E. moritzii*, Hagsater 5075 (Balogh); *E. moyabambae*, Hagsater 6546 (AMO); *E. myrianthum*, Hagsater 5085 (AMO); *E. nagelii*, Hagsater 4735 (AMO); *E. nocturnum*, Lamas s.n. (Balogh); *E. nonanisatum*, Hagsater 5887 (AMO); *E. nutans*, Hagsater 5208 (AMO); *E. oaxacanum*, Hagsater 5753 (AMO); *E. oerstedii; E. omissum*, Greenwood s.n. (AMO); *E. otavalo*, Hagsater 5914 (AMO); *E. pachyrachis*, Hagsater 6384 (AMO); *E. patens*, Behib 709 (Balogh); *E. parkinsonianum*, Behib s.n. (Balogh); *E. porpax* (Neolehmannia), Dressler s.n. (Balogh); *E. propinquum*, Hagsater s.n. (AMO); *E. pugioniforme*, Hagsater s.n. (AMO); *E. obesum*, Hagsater 6330 (AMO); *E. radicans*, Balogh s.n. (US); *E. radioferens*, Hagsater 4515 (AMO); *E. ramosum*, Hagsater 5596 (AMO); *E. rowleyi*, Hagsater 4827 (US); *E. sanchoi*, Hagsater 6459 (AMO); *E. scriptum*, Hagsater 5907 (AMO); *E. silacayoapan*, Hagsater 6030 (AMO); *E. skutchii*, Hagsater 6259 (AMO); *E. stanifordianum*, Hagsater s.n. (AMO); *E. subviolascens*, Hagsater 5778 (AMO); *E. turialvae*, Hagsater 6419 (AMO); *E. vescicatum*, Hagsater 6149 (AMO); *E. viejii*, Hagsater 5348 (AMO). *Epipogium aphyllus*, Baenitz s.n. (US); *E. roseum*, Nicholson 179 (US). *Epistephium amplexicaule*, Barriga 08293 (US), Britton and Rusby 2908 (US). *Eria inornata*, Clements 2344 (NCBG); *E. paniculata*, Dressler s.n. (Missouri Botanical Garden). *Eriaxis rigida*, Buchholz 1003 (US), McKee 3302 (US).

Flickingeria comata, SH 1149 (Balogh).

Galeola casythoides, Helms 11-1900 (US). *Gastrodia elata*, Teng 90332 (US); *G. sesamoides*, Bernhardt s.n. (Balogh). *Glomera obtusa*, Dressler s.n. (Balogh). *Glossorhyncha* sp., Dressler s.n. (Balogh).

Hagsatera brachycolumna, McCullough 77-37 (Balogh). *Hexalectris brevicaulis*, Greenwood 1059 (AMO). *Hexisea bidentata*, Balogh 731 (Balogh). *Hippeophyllum scotechini*, Sinclair 5651(US). *Homalopetalum pumilo*, Hagsater 73 (AMO).

Isochilus sp., Hagsater 5808 (AMO); *I. aurantiaca*, Hagsater 4518 (AMO); *I. linearis*, Balogh 719 (US); *I. major*, Montebello s.n. (Balogh).

Jacquinella cobanensis, Balogh s.n. (Balogh); *J. equitantifolia*, Miller s.n. (Balogh); *J teres*, Balogh s.n. (Balogh).

Koellensteinia kellneriana, Dressler s.n. (Balogh).

Laelia albida, Pollard s.n. (AMO), Balogh s.n. (Balogh); *L. anceps*, Pollard s.n. (AMO); *L. autumnalis*, Greenwood s.n. (AMO); *L. cinnabarina* (SI 801097); *L. dickinsonii*, Hagsater 5708 (AMO); *L. flava* (SI 78246); *L. furfuracea*, Greenwood s.n. (AMO); *L. gouldiana*, Hagsater 10–78 (AMO); *L. xanthrotropis*, Moore s.n. (Balogh). *Laeliopsis domingensis*, Hagsater s.n. (AMO). *Lecanorchis brachycarpa*, Ohiui and Walker 7023 (US). *Lepanthes* sp., Balogh 882 (Balogh). *Liparis draculoides*, Greenwood 983 (AMO); *L. elata*, Greenwood 759 (AMO); *L. galeottiana*, Greenwood 889 (AMO); *L. lilifolia*, Balogh s.n. (US); *L. reflexa*, SH 1139 (Balogh).

Malaxis carnosa, Greenwood 717 (AMO); *M. latifolia*, SH 1143 (Balogh); *M. lepidota*, Greenwood 903 (AMO); *M. marsupichila*, Clements 1148 (NCBG); *M. soulei*, Greenwood 811 (AMO); *M. fastigata*, Greenwood 626 (AMO); *M. javesiae*, Greenwood 1068 (AMO); *M. rosei*, Greenwood s.n. (AMO). *Masdevallia aureopurpurea* (SI 79187); *M. brachyura* (SI) 792270); *M. cibilis* (SI 78292); *M. infracta* (SI); *M. uniflora*, Balogh s.n. (Balogh). *Meiracyllium trinasutum*, Dressler s.n. (Balogh). *Monophyllorchis maculeatus*, Dressler s.n. (Balogh).

Nervilia aragoana, Fosberg 37453 (US); *N. plicata*, Saldanka and Ramamoorthy 1706 (US). *Nidema boothiana*, Balogh 802 (Balogh).

Oberonia emarginata, King 5550 (US), *O. japonica*, Makino s.n. (US). *Octarrhena condensata*, Dressler s.n. (Balogh). *Octomeria graminifolia* (SEL). *Oestedella myriantha*, Hagsater s.n. (AMO); *O. pajetense*, Hagsater s.n. (AMO); *O. pinnifera*, Hagsater 6502 (AMO); *O. ramosum*, Hagsater s.n. (AMO); *O. schweinfurthianum*, Hagsater 4351 (AMO); *O. wallisci*, Tschen and Hagsater s.n. (AMO).

Palmorchis sp., Dressler s.n. (AMO); *P. trilo-*

bulata, Dressler 3683 (Balogh). *Phaius australis*, Clements 2345 (NCBG). *Pholidota* sp. (SEL); *P. pallida*, Clements 2304 (NCBG). *Phreatia robusta* (Rhynchophreatia), Clements 2347 (NCBG). *Physinga* sp., Hagsater 5289 (AMO); *P. physodes*, Hagsater s.n. (AMO). *Physosiphon tubatus* (SEL 41-76-5). *Physothallis harlingii* (SEL 44-75-240). *Platystele stenostachya* (SEL 114-76-6). *Pleurothallis* sp., Balogh 888 (Balogh); *P. caespitosa* (SI 79594); *P. ghiesbrichtiana*, unknown (Balogh); *P. longissima*, Balogh s.n. (Balogh). *Pogonia ophioglossoides*, Mearns 69 (US), Smith 205 (US). *Ponera striata*, Balogh s.n. (Balogh). *Pseudoepidendrum spectabile*, Hagsater 3390 (AMO). *Psilochilus* sp., Dressler s.n. (Balogh).

Restrepia xanthophthelma (SEL 123-76-74). *Rhyncholaelia glauca*, Jackson s.n. (Balogh).

Scaphyglottis sp. (SI); *S.* sp., Balogh 833 (Balogh). *Scaphosepalum sardinata* (SEL 30-74-207). *Schomburgkia superbiens*, Jones s.n. (Balogh); *S. lueddemannii*, Concavas s.n. (Balogh); *S. tubicinis*, Greenwood s.n. (AMO); *S. wendlandii*, unknown (Balogh). *Sirhookera lanceolata*, Saldanka and Ramamoorthy 562 (US); *S. latifolia*, Jarrett, Saldanka, and Ramamoorthy 696 (US). *Sobralia amabilis*, Dressler s.n. (Balogh); *S. decora*, Dodson s.n. (SEL); *S. fenzliana*, Dressler s.n. (Balogh); *S. fragrans* (SI); *S. macrantha* (SI). *Stenoglossum coryophorum*, Dressler s.n. (Balogh). *Stereosandra javanica*, Ramos 12124 (US), Fosberg 37285 (US). *Sunipia bicolor*, Rock 7070 (US); *S. racemosa*, Dressler s.n. (Balogh); *S. scariosa*, Forrest 26732 (US).

Thelasis carinata, Clements 2306 (NCBG). *Thunia alba*, Troth 880 (US). *Triphora trianthophora*, Luer s.n. (SEL).

Vanilla sp. (SEL); *V. edwardii*, Reitiz and Klein s.n. (US); *V. pauciflora*, Dressler s.n. (Balogh); *V. planifolia* SEL.

Wullschlaegelia aphylla, Dressler 4940 (Balogh); *W. calcarata*, Dressler 4646 (MO).

Xyllosum pallidiflora, unknown (Balogh).

Yoania japonica, Mykosan (US).

VANDOID GROUP.—*Acampe multiflora* (SEL 81-1049). *Acineta blanca*, Mejia s.n. (Balogh). *Acriopsis javanica*, cultivated (Balogh); *A. nelsoniana*, Dressler s.n. (Balogh). *Ada* sp., Schmidt s.n. (Balogh). *Aerangis friesorum* SI 81509. *Aeranthes* sp., (SEL 78-149). *Aerides mitratum* (SI 7812). *Angraecum distichum* (SEL); *A. magdalense*, (SEL 78-380). *Anguloa cliftonii*, Escobar s.n. (Balogh). *Arachnis flosaeris* (SI). *Aspasia epidendroides*, Dressler s.n. (Balogh); *A. principissa*, Dressler s.n. (Balogh).

Bollea lalindei, Mejia s.n. (Balogh). *Brassia arcuigera* (SEL); *B. gireoudiana* (SEL); *B. maculata*, (SI); *B. signata*, Suarez s.n. (AMO).

Camaridium imbricatum (SI 781056). *Campylocentrum micranthum*, Foster s.n. (Balogh). *Catasetum callosum*, Dressler s.n. (Balogh); *C. crystianum*, (SEL); *C. expansum*, (SEL); *C. integerimum*, Jones s.n. (SEL); *C. luridum*, Dressler s.n. (Balogh); *C. macrocarpum*, Balogh s.n. (Balogh); *C. roseum*, Dressler s.n. (Balogh); *C. saccatum*, Pabst s.n. (Balogh); *C. sanguineum*, (SEL); *C. viridiflavum*, Balogh 830 (Balogh). *Centropetalum sanguineum*, (SEL). *Ceratostylis rubra*, (SI 7883); *Chondrorhyncha discolor*, (SI 79820). *Cirrhaea saccata*, (SEL). *Cleisostoma macrantha*, (SI 7811e50). *Clowesia russelliana*, (SEL); *C. warsceswezii*, Balogh s.n. (Balogh), Dressler s.n. (Balogh). *Cochleanthes discolor* (SEL). *Comparettia macroplectron* (SI 79325). *Corallorhiza striata*, Balogh 977 (US). *Coryanthes maculata*, Dressler s.n. (Balogh). *Cryptarrhena lunata*, Dressler s.n. (Balogh). *Cycnoches chlorochilon*, Balogh 877 (Balogh); *C. diandre*, Dressler s.n. (Balogh); *C. egertonianum* (SEL); *C. loddigessii* (SEL); *C. ventrycossum*, Dressler s.n. (Balogh); *C. warscewiczii*, Suarez s.n. (Balogh); *C.* sp., Suarez 391 (AMO). *Cymbidium* sp. (SI); *C. caniculatum*, SH 1144 (NCBG); *C. eburneum*, (SI 79840). *Cyrtochilum carderi*, Posada s.n. (Balogh). *Cyrtopodium punctatum* (SI). *Cyrtorchis monteirae* (SI 792172).

Dichaea morrisii, Dressler s.n. (Balogh); *D. panamensis*, Dressler s.n. (Balogh). *Dipodium punctatum*, Clements 2272 (NCBG); *D. pandanum*, Dressler s.n. (Balogh). *Doritis pulcherrima* (SEL). *Dressleria helleri*, Balogh s.n. (Balogh).

Eriopsis wercklei, Dressler 3940 (Balogh). *Erycina echinata*, Dressler s.n. (Balogh). *Eulophia faireana*, Dressler s.n. (Balogh); *E. petersii*, unknown

(Balogh); *E. tuberosa*, Dressler s.n. (Heidelberg).

Fernandezia hartwegii, Dressler s.n. (Balogh); *F. sanguinea*, Dressler s.n. (Balogh).

Galeandra devonianum (SI). *Gastrochilus bellinus* (Frankfurt). *Genyorchis pumila* (Utrecht). *Geodorum* sp., Dressler s.n. (Balogh). *Gomesa crispa* (SI 78220). *Gomeza planifolia* (SI 792196). *Gongora claviodora*, Dressler s.n. (Balogh); *G. gratulabunda*, Mejia s.n. (Balogh); *G.* sp., Suarez 169 (AMO); *G. tricolor* (SEL 1-1975-618); *G. truncata* (SEL 105-76-25). *Govenia bella*, Greenwood 956 (AMO); *G. capitata*, Greenwood 873 (AMO); *G. lagenophora*, Greenwood 417 (AMO); *G. liliacea*, Greenwood 556 (AMO); *G. mutica*, Greenwood 574 (AMO); *G. superba*, Greenwood 902 (AMO); *G. tequiliana*, Dressler and Hagsater 2715 (AMO).

Haraella odorata (SI). *Houlletia tigrina*, Mejia s.n. (Balogh). *Huntleya burtii*, Balogh s.n. (Balogh).

Ionopsis utricularioides, Dressler s.n. (Balogh).

Jumellea sagittata (SI 78234).

Kefersteinia parvilabris, Mejia s.n. (Balogh). *Kegeliella kepperi*, Dressler s.n. (Balogh). *Koellensteinia kellneriana*, Dressler s.n. (Balogh).

Listrostachys pertusa, Dressler s.n. (Heidelberg). *Lockhartia micrantha*, Balogh 581 (Balogh); *L. oestedii*, Dressler s.n. (Balogh); *L. pallida*, Dressler s.n. (Balogh). *Lueddmannia pescatorei*, Mejia s.n. (Balogh). *Lycaste aromatica* (SI 811874); *L. consobrina* (SI 76960); *L. cruenta*, Hagsater s.n. (AMO); *L. deppei*, Suarez s.n. (AMO); *L. leucantha* (SI); *L. powellii*, Dressler 3867 (Balogh).

Masdevallia asperrima (SI 812667). *Maxillaria brunnea*, Dressler s.n. (Balogh); *M. juergensii* (SI 77118); *M. rufescens*, Balogh s.n. (Balogh). *Mexicoa ghiestbrechtiana*, Balogh 970 (Balogh). *Miltonia* "Anne Warne" (SEL); *M. bluntii* (SI); *M. flavescens* (SI 78319); *M. spectabilis* (SI 78321-A). *Miltoniopsis roezlii*, Dressler 4084 (MO). *Mormodes cartonii*, Balogh 811 (Balogh). *Mormolyca ringens*, Dressler s.n. (Balogh).

Neobenthamia (SI 76404). *Notylia maculilabris*, Dressler 1096 (MO); *N. trisepala*, (SI 78331).

Oberonia emarginata, King 5550 (US). *Odontoglossum* sp., Hagsater 43109 (AMO); *O. apterum*, Greenwood s.n. (AMO); *O. cordatum*, Halbinger s.n. (Balogh); *O. harryanum*, Dressler s.n. (Balogh); *O. maculatum*, Balogh s.n. (Balogh); *O. majace*, Hagsater 5341 (AMO); *O. pulchellum* Balogh s.n. (Balogh); *O. reichenheimii*, Balogh 970 (US). *Oeceoclades maculata*, Foster s.n. (Balogh). *Oncidium aurisassinarum* (SI 797005); *O. desertorum*, Stern 216 (Balogh); *O. durangensis*, Hagsater 3769 (AMO); *O. fasciculatum*, Hagsater 5332 (AMO); *O. leucochilum*, (SEL); *O. maculatum*, Pollard s.n. (AMO); *O. oblongatum*, Hagsater 3364 (AMO); *O. obryzatum*, Hagsater 4177 (AMO); *O. ornithorrhynchum*, Pollard s.n. (AMO); *O. papilio* (SI); *O. reflexum*, Balogh 789 (Balogh); *O. stenotis* (SI 76251). *Ornithocephalus bicornis*, Balogh 840 (Balogh); *O. cochlearaeformis*, Balogh s.n. (Balogh); *O. tripterus*, Dressler s.n. (Balogh). *Ornithophora radicans*, Dressler s.n. (Balogh). *Osmoglossum egertonii*, Hagsater 6518 (AMO); *O. pulchellum*, Pollard s.n. (AMO).

Pachyphyllum distichum, Hutchison 6655 (US); *P. pasti*, Holmgren s.n. (US); *Paradisianthus micranthus* (SEL); *Peristeria elata*, Balogh s.n. (Balogh). *Phalaenopsis corni-cervi* (SI 781076); *P. luemanniana*, Brecht 1969 (Balogh). *Plectrophora alata*, JFM 882 (Balogh); *P. cultifolia* (SI 781440). *Polycynis gratiola*, unknown (Balogh); *P. adansonae* (SI 792259); *P. bella* (Missouri Botanical Garden). *Polystachya concreta* (SI 7774); *P. galangoreae* (SI); *P. tessellata* (SI 792260).

Rangaeris amaniensis, Dressler s.n. (Balogh). *Renanthera imschootiana*, Dressler s.n. (Balogh). *Rhynchostylis retusa*, Dressler s.n. (Balogh). *Rodriguezia granadensis*, Dressler s.n. (Balogh). *Rossioglossum schlieperianum*, Hagsater 6433 (AMO); *R. splendens*, Hagsater 3893 (AMO); *R. williamsianum*, Hagsater 6630 (AMO).

Sarcanthus pachyphyllus (SI 792146). *Schomburgkia tubicinis* (SEL). *Sievekingia burcheri*, Dressler s.n. (Balogh); *S. columbiana*, Dressler s.n. (Balogh). *Sigmatosalix guatemalensis*, Lent s.n. (Balogh); *S. mexicana*, Hagsater 4772 (AMO); *S.* sp. Balogh 814 (Balogh). *Stanhopea connata* (SI 791282); *S. costaricensis*, Dressler s.n. (Balogh); *S. ecornuta*, Dressler 4092 (Balogh); *S. guttulata* (SI); *S. oculata*, Suarez 82 (AMO); *S. tricornis*, Dressler s.n. (Balogh); *S. tigrina*, Dressler s.n. (Balogh); *S. wardii*, Dressler s.n. (Balogh). *Stelis* sp., Balogh 893 (Balogh). *Stenocoryne racemosa* (SI 78477); *S. vitellina*, Dressler s.n. (Balogh).

Telipogon klotscheanus, Dressler s.n. (Balogh). *Teuscheria dodsonii*, Dressler s.n. (Balogh). *Thecostele alata*, Dressler s.n. (Balogh); *T. maingayi*, Dressler s.n. (Balogh). *Thrixospermum elongatum* (SI 791401). *Tipularia discolor*, Balogh 908 (US). *Trichocentrum bursigera*, unknown (Balogh); *T. pfavii*, Balogh s.n. (Balogh); *T. tigrinum* (SEL). *Trichoglottis fasciata* (SEL). *Trichopilia elegans* (SI 78486); *T. galeottiana* (SI 78487); *T. hennisiana*, Mejia s.n. (Balogh). *Trigonidium egertonianum*, Pollard s.n. (AMO). *Trizeuxis falcata* (SI 792008).

Vanda coerulescens (SI 781461); *V.* sp. (SI); *V. limbata* (SEL 26-75-3). *Vandopsis lissochiloides* (SEL).

Warcella cyanea, Mejia s.n. (Balogh). *Warmingia* sp. (SEL); *W. elegans*, Dressler s.n. (Balogh). *Warscewiczella velata*, Lasca s.n. (Balogh).

Xylobium colleyi, Dressler 3748 (Balogh); *X. corrugatum*, Mejia s.n. (Balogh); *X. elongatum* (SI 791004); *X. foveatum* (SI 791005).

Zygopetalum mackey (SI 76956).

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PLATE 1.—Floral morphology of Orchidaceae, whole flowers: *a, Neuwiedia veratifolia* Blume, photo by J.B. Comber; *b, Apostasia wallichii* R. Brown, J.B. Comber; *c, Cypripedium irapeanum* Llave and Lexarza, E.W. Greenwood; *d, Paphiopedilum venustum* Pfitzer, P. Burns-Balogh; *e, Paphiopedilum spicereanum* Pfitzer, P. Burns-Balogh; *f, Diuris longifolia* R. Brown, M.A. Clements; *g, Prasophyllum parvifolium* Lindley, M.A. Clements; *h, Cryptostylis javanica* J.J. Smith, J.B. Comber; *i, Anoectochilus setaceus* Lindley, J.B. Comber; *j, Erythrodes* sp., E.W. Greenwood; *k, Ponthieva tuerkheimii* Schlechter, E.W. Greenwood; *l, Caladenia patersonii* R. Brown, M.A. Clements; *m, Thelymitra nuda* R. Brown, M.A. Clements; *n, Platanthera ciliaris* Lindley, P. Burns-Balogh; *o, Habenaria koordersii* J.J. Smith, J.B. Comber; *p, Habenaria distans* Grisebach, E.W. Greenwood.

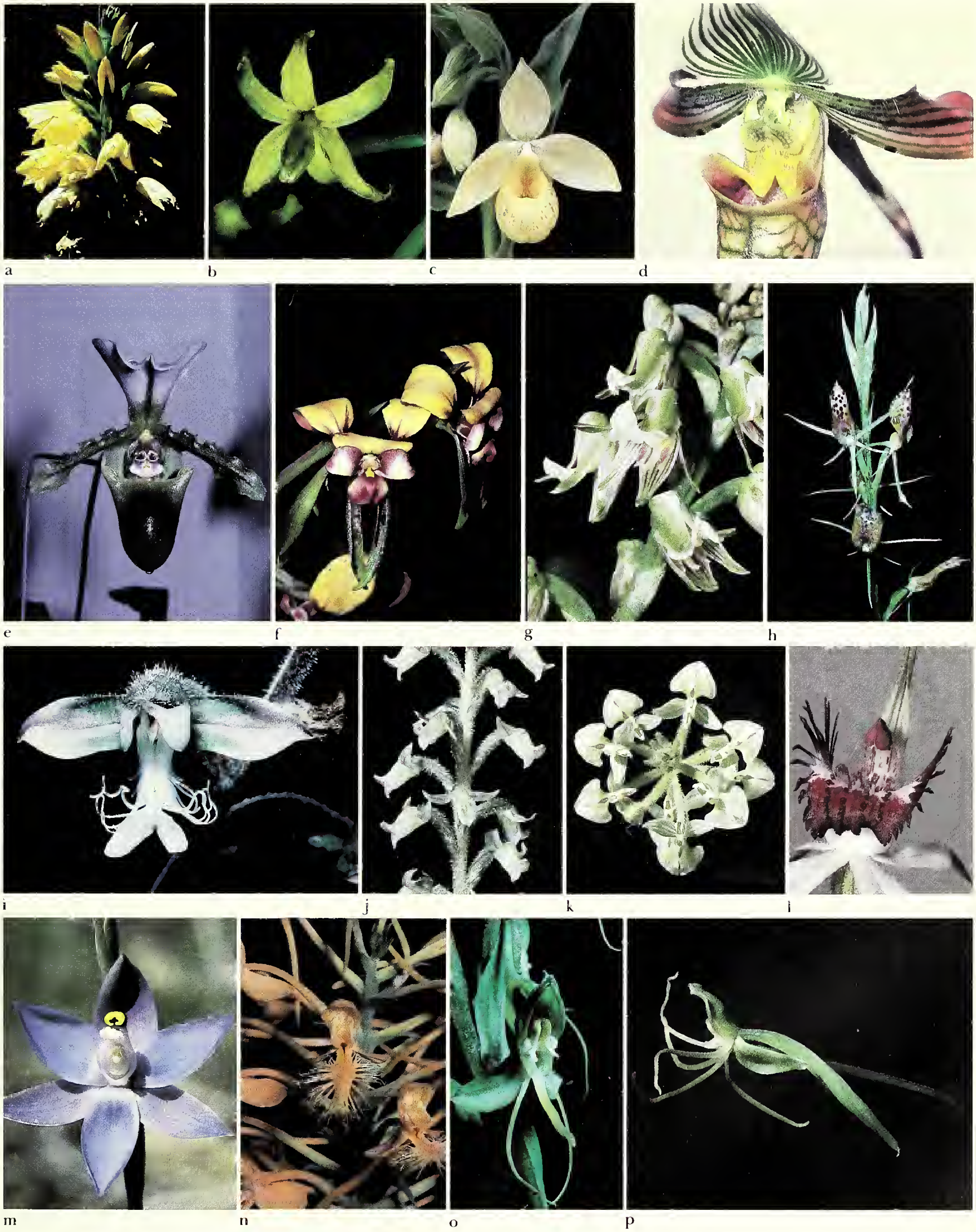
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PLATE 2.—Floral morphology of Orchidaceae, whole flowers: *a, Galearis spectabilis* Rafinesque, P. Burns-Balogh; *b, Disperis javanica* J.J. Smith, J.B. Comber; *c, Arundina graminifolia* Hochinger, J.B. Comber; *d, Bletia* sp., E.W. Greenwood; *e, Hexalectris brevicaulis* L.O. Williams, E.W. Greenwood; *f, Pleurothallis* sp., E.W. Greenwood; *g, Stelis* sp., P. Burns-Balogh; *h, Mormodes ignea* Lindley and Paxton, P. Burns-Balogh; *i, Oncidium* sp., E.W. Greenwood; *j, Clowesia thylaciochila* (Lemoire) Dodson, E.W. Greenwood; *k, Clowesia warscewitzii* (Lindley and Paxton) Dodson, P. Burns-Balogh; *l, Cynoches warscewitzii* Reichenbach filius, E.W. Greenwood; *m, Catasetum sanguineum* Lindley (♀), P. Burns-Balogh; *n, Catasetum sanguineum* Lindley (♂), P. Burns-Balogh.


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PLATE 3.—Floral morphology of Orchidaceae, dissected parts of flowers: *a, Cypripedium acaule* Aiton, P. Burns-Balogh; *b, Sarcoglottis gutturosa* (Reichenbach filius) Ames, E.W. Greenwood; *c–f, Sarcoglottis pauciflora* (Richard and Galeotti) Schlechter, E.W. Greenwood; *g,h, Ponthieva tuerckheimii* Schlechter, E.W. Greenwood; *i, Ponthieva racemosa* (Walter) Mohr, E.W. Greenwood; *j, Rhizanthella gardneri* Rogers, P. Burns-Balogh; *k, Habenaria distans* Grisebach, E.W. Greenwood; *l, Bletia ensifolia* L.O. Williams, E.W. Greenwood; *m, Hexalectris brevicaulis* L.O. Williams, E.W. Greenwood; *n, Pleurothallis tribuloides* (Swartz) Lindley, E.W. Greenwood.

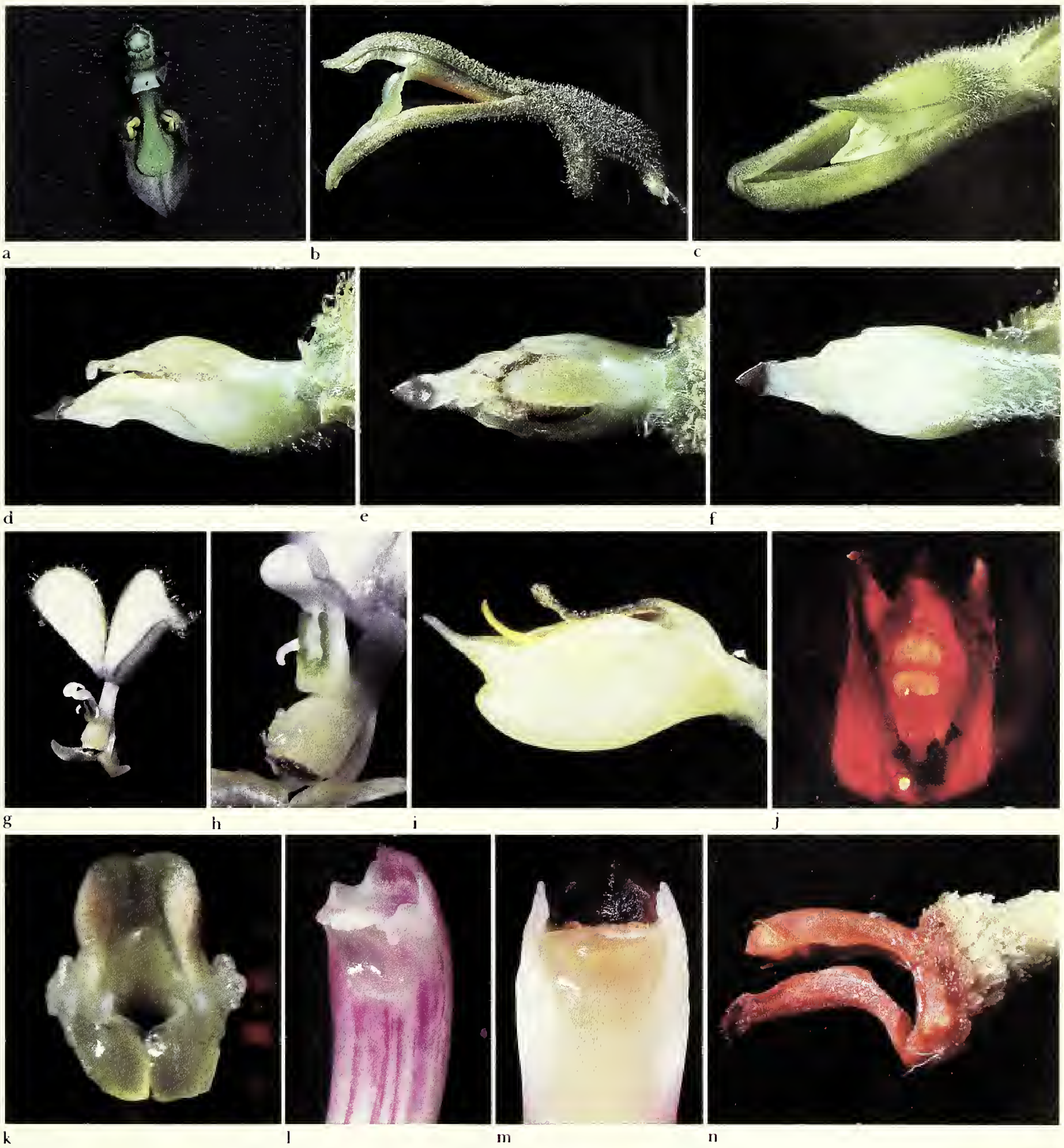
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PLATE 4.—Floral morphology of Orchidaceae, dissected parts of flowers: *a, Lepanthes* sp., P. Burns-Balogh; *b, Oncidium* sp., E.W. Greenwood; *c, Clowesia thylaciochila* (Lemoire) Dodson, E.W. Greenwood; *d, Cycnoches warscewitzii* Reichenbach filius, E.W. Greenwood; *e–g, Gongora truncata* Lindley, E.W. Greenwood; *h–k, Stanhopea oculata* (Loddigues) Lindley, E.W. Greenwood.


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